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A TEXT BOOK

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BY

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WITH ILLUSTRATIONS.

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PART III.

The Central Nervous System.

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I AM of course aware of the disadvantages of issuing this edition of my Text Book in instalments, and very much regret that this part does not complete the work. The failure to get the whole of the remainder ready has been due to lack, not of will, but of ability and opportunity.

I take this opportunity of thanking my friend Dr Gowers, for the loan of two woodcuts, as well as for much valuable advice. Throughout the whole of this part I have been largely assisted by my colleague Mr Langley, and by my friend and former pupil Dr Sherrington. The latter, besides helping me with criticisms, has prepared for me most of the figures after original drawings by himself. What little merit there may be in this part is largely due to these two gentlemen.

M. FOSTER.

CAMBRIDGE,
September, 1890.

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BOOK III.

THE CENTRAL NERVOUS SYSTEM AND ITS INSTRUMENTS.

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CHAPTER I.

THE SPINAL CORD.

SEC. 1. ON SOME FEATURES OF THE SPINAL NERVES.

§ **558.** WE have called the muscular and nervous tissues the master tissues of the body; but a special part of the nervous system, that which we know as the central nervous system, the brain and spinal cord, is supreme among the nervous tissues and is master of the skeletal muscles as well as of the rest of the body. We have already (Book I. Chap. III.) touched on some of the general features of the nervous system, and have now to study in detail the working of the brain and spinal cord. We have to inquire what we know concerning the laws which regulate the discharge of efferent impulses from the brain or from the cord, and to learn how that discharge is determined on the one hand by intrinsic changes originating, apparently, in the substance of the brain or of the cord, and on the other hand by the nature and amount of the afferent impulses which reach them along afferent nerves.

As we shall see the study of the spinal cord cannot be wholly separated from that of the brain, the two being very closely related. Nevertheless it will be of advantage to deal with the spinal cord by itself as far as we can. The medulla oblongata or spinal bulb[1] we shall consider as part of the brain. But before we speak of the spinal cord itself, it will be desirable to say a few words concerning the spinal nerves, that is to say the nerves which issue from the spinal cord.

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[1] The term medulla oblongata is not only long, but presents difficulties, since the word medulla is now rarely used to denote the whole spinal cord (medulla spinalis) but is generally used to denote the peculiar coat of a nerve fibre, the white substance of Schwann. In using instead the word *bulb* or if necessary, *spinal bulb* there is little fear of confusion with any other kind of bulb. The adjective is in not uncommon use, in such phrases as 'bulbar paralysis.'

We have already seen (§ 96) that each of the spinal nerves arises by two roots, an anterior root attached to the ventral or anterior surface, and a posterior root attached to the dorsal or posterior surface of the cord. We have further seen that the latter bears a ganglion, a 'ganglion of the posterior root' or 'spinal ganglion,' and we have (§ 97) studied the structure of this ganglion.

We stated at the same time that while the trunk of a spinal nerve contained both efferent and afferent fibres, the efferent fibres were gathered up into the anterior root and the afferent fibres into the posterior root; but we gave no proof of this statement.

§ **559**. Before we proceed to do so, it will be as well to say a few words on the terms 'efferent' and 'afferent.' By efferent nerve fibres we mean nerve fibres which in the body usually carry impulses from the central nervous system to peripheral organs. Most efferent nerve fibres carry impulses to muscles, striated or plain, and the impulses passing along them give rise to movements; hence they are frequently spoken of as 'motor' fibres. But all efferent fibres do not end in or carry impulses to muscular fibres; we have seen for instance that some efferent fibres are secretory. Moreover all the nerve fibres going to muscular fibres do not serve to produce movement; some of them, as in the case of certain vagus fibres going to the heart, are inhibitory and may serve to stop movement.

By 'afferent' nerve fibres we mean nerve fibres which in the body usually carry impulses from peripheral organs to the central nervous system. A very common effect of the arrival at the central nervous system of impulses passing along afferent fibres is that change in consciousness which we call a 'sensation'; hence afferent fibres or impulses are often called 'sensory' fibres or impulses. But as we have already in part seen, and as we shall shortly see in greater detail, the central nervous system may be affected by afferent impulses, and that in several ways, quite apart from the development of any such change of consciousness as may be fairly called a sensation. We shall see reason for thinking that afferent impulses reaching the spinal cord, and indeed other parts of the central nervous system, may modify reflex or automatic or other activity without necessarily giving rise to a "sensation." Hence it is advisable to reserve the terms 'efferent' and 'afferent' as more general modes of expression than 'motor' or 'sensory.'

We have seen in treating of muscle and nerve, that the changes produced in the muscle serve as our best guide for determining the changes taking place in a motor nerve; when a motor nerve is separated from its muscle (§ 72) the only change which we can appreciate in it is an electrical change. Similarly in the case of an afferent nerve, the central system is our chief teacher; in a bundle of afferent fibres isolated from the central nervous system, in a posterior root of a spinal nerve for instance, the only change which we can appreciate is an electrical change. To learn the characters of afferent impulses we must employ the central nervous system. But in this we meet with difficulties. In studying the phenomena of motor nerves we are greatly assisted by two facts. First, the muscular contraction by which we judge of what is going on in the nerve is a comparatively simple thing, one contraction differing from another only by such features as extent or amount, duration, frequency of repetition and the like, and all such differences are capable of exact measurement. Secondly, when we apply a stimulus directly to the nerve itself, the effects differ in degree only from those which result when the nerve is set in action by natural stimuli, such as the will. When we come, on the other hand, to investigate the phenomena of afferent nerves, our labours are for the time rendered heavier, but in the end more fruitful, by the following circumstances:—First, when we judge of what is going on in an afferent nerve by the effects which stimulation of the nerve produces in some central nervous organ, in the way of exciting or modifying reflex action, or modifying automatic action, or affecting consciousness, we are met on the very threshold of every inquiry by the difficulty of clearly distinguishing the events which belong exclusively to the afferent nerve from those which belong to the central organ. Secondly, the effects of applying a stimulus to the peripheral end-organ of an afferent nerve are very different from those of applying the same stimulus directly to the nerve-trunk. This may be shewn by the simple experience of comparing the sensation caused by bringing any sharp body into contact with a nerve laid bare in a wound with that caused by contact of an intact skin with the same body. These and like differences reveal to us a complexity of impulses, of which the phenomena of motor nerves gave us hardly a hint.

We shall further see in detail later on that our consciousness may be affected in many different ways by afferent impulses; we must distinguish not only sensory from other afferent impulses, but also different kinds of sensory impulses from each other. Certain afferent nerves are spoken of as nerves of special sense, and the nature of the afferent impulses passing along these special nerves together with the modifications of consciousness caused by arrival of these impulses at the central nervous system constitute by themselves a complex and difficult branch of study. In some of the problems connected with the central nervous system we shall have to appeal to the results of a study of these special senses; but, on the other hand, a knowledge of the central nervous system is necessary to a proper understanding of the special senses; and on the whole it will be more convenient to study the former before the latter.

We may, however, digress here to remark that the question whether an afferent impulse differs in itself from an efferent impulse is one of great difficulty. It is true that the electrical changes, which alone as we have said we can appreciate in an isolated piece of nerve, appear to be the same in both kinds of fibres; in each the electrical change is propagated in both directions and possesses the same features. But it would be hazardous to insist too much on this. Moreover, we must remember that what we call a nervous impulse, especially one provoked by artificial stimulation, constitutes a gross change in the nerve fibre, and that changes of a finer, more delicate nature, such as cannot be shewn by the coarse methods used to detect a 'nervous impulse,' may take place in, and be propagated along, a nerve fibre. We shall have occasion immediately to point out that the condition of an afferent nerve fibre along its whole length is dependent on a nerve cell in the ganglion of the posterior root; the fibre when cut off from the nerve cell degenerates and dies. This means that in the intact fibre certain influences are propagated along the fibre from the cell in the ganglion to the peripheral endings of the fibre, that is to say in a direction the opposite of that taken by the ordinary afferent nervous impulses; and it may be that in like manner in efferent fibres some influences are propagated centripetally from the peripheral endings to the central nervous system. Our knowledge of these influences is extremely limited; but it is important to bear in mind the possibility of their occurrence. And we had this in view, when above, in speaking of efferent and afferent fibres, we used the phrase "usually carry impulses."

§ **560**. The proof that the afferent and efferent fibres which are both present in the trunk of a spinal nerve are parted at the roots, the efferent fibres running exclusively in the ventral or anterior root and the afferent fibres exclusively in the dorsal or posterior root, is as follows.

When the anterior root is divided, the muscles supplied by the nerve cease to be thrown into contractions either by the will, or by reflex action, while the structures to which the nerve is distributed retain their sensibility. During the section of the root, or when the proximal stump, that connected with the spinal cord, is stimulated, no sensory effects are produced. When the distal stump is stimulated, the muscles supplied by the nerve are thrown into contractions. When the posterior root is divided, the muscles supplied by the nerve continue to be thrown into action by an exercise of the will or as part of a reflex action, but the structures to which the nerve is distributed lose the sensibility which they previously possessed. During the section of the root, and when the proximal stump is stimulated, sensory effects are produced. When the distal stump is stimulated no movements are called forth. These facts demonstrate that sensory impulses pass exclusively by the posterior root from the peripheral to the central organs, and that motor impulses pass exclusively by the anterior root from the central to the peripheral organs; and as far as our knowledge goes the same holds good not only for sensory and motor but also for afferent and efferent impulses.

An exception must be made to the above general statement, on account of the so-called "recurrent sensibility" which is witnessed in conscious mammals, under certain circumstances. It sometimes happens that when the distal stump of the divided anterior root is stimulated, signs of pain are witnessed. These are not caused by the concurrent muscular contractions or cramp which the stimulation occasions, for they persist after the whole trunk of the nerve has been divided some little way below the union of the roots above the origins of the muscular branches, so that no contractions take place. They disappear when the posterior root is subsequently divided, and they are not seen if the mixed nerve-trunk be divided close to the union of the roots. The phenomena are probably due to the fact, that bundles of sensory fibres of the posterior root after running a short distance down the mixed trunk turn back and run upwards in the anterior root, (being distributed probably to the pia mater) and by this recurrent course give rise to the recurrent sensibility.

§ **561.** Concerning the *ganglion* on the posterior root, we may say definitely that we have no evidence that it can act as a centre of reflex action; nor have we any evidence that it can spontaneously give origin to efferent impulses and thus act as an automatic centre, as can the central nervous system itself. The bodies of the nerve cells behave somewhat differently from the axis cylinders at some distance from the cells, though, as we have seen, these are in reality processes of the nerve cells; thus the nerve cells in the ganglion appear to be more sensitive to certain poisons than are the nerve fibres of the nerve-trunk. But beyond this, our knowledge concerning the function of the ganglion is almost limited to the fact that it is in some way intimately connected with the nutrition of the nerve. As we have already (§ 83) said, when a mixed nerve-trunk is divided the peripheral portion degenerates from the point of section downwards towards the periphery. The central portion does not so degenerate, and if the length of nerve removed be not too great, the central portion may grow downwards along the course of the degenerating peripheral portion, and thus regenerate the nerve. This degeneration is observed when the mixed trunk is divided in any part of its course from the periphery to close up to the ganglion. When the posterior root is divided between the ganglion and the spinal cord, the portion attached to the spinal cord degenerates, but that attached to the ganglion remains intact. When the anterior root is divided, the proximal portion in connection with the spinal cord remains intact, but the distal portion between the section and the junction with the other root degenerates; and in the mixed nerve-trunk many degenerated fibres are seen, which, if they be carefully traced out, are found to be motor (efferent) fibres. If the posterior root be divided carefully between the ganglion and the junction with the anterior root, the small portion of the posterior root left attached to the peripheral side of the ganglion above the section remains intact, as does also the rest of the root from the ganglion to the spinal cord, but in the mixed nerve-trunk are seen numerous degenerated fibres, which when examined are found to have the distribution of sensory (afferent) fibres. Lastly, if the posterior ganglion be excised, the whole posterior root degenerates, as do also the sensory (afferent) fibres of the mixed nerve-trunk. Putting all these facts together, it would seem that the growth of the efferent and afferent fibres takes place in opposite directions, and starts from different nutritive or 'trophic' centres. The afferent fibres grow away from the ganglion either towards the periphery, or towards the spinal cord. The efferent fibres grow outwards from the spinal cord towards the periphery. This difference in their mode of nutrition is frequently of great help in investigating the relative distribution of efferent and afferent fibres. When a posterior root is cut beyond the ganglion, or the ganglion excised, all the afferent nerves degenerate, and in the mixed nerve-branches these afferent fibres, by their altered condition, can readily be traced. Conversely, when the anterior roots are cut, the efferent fibres alone degenerate, and can be similarly recognized in a mixed nerve-tract. When the anterior root is divided some few fibres in it do not, like the rest, degenerate, and when the posterior root is divided, a few fibres in the anterior root are seen to degenerate like those of the posterior root; these appear to be the fibres which give to the anterior root its "recurrent sensibility." In the case of certain spinal nerves at all events, it has also been ascertained that when the posterior root is divided, while most of the fibres in the part of the root thus cut off from the ganglion but left attached to the cord degenerate, some few do not. These few appear to have their trophic centre not in the ganglion, but in some part of the spinal cord itself; we shall refer to these later on.

This method of distinguishing nerve fibres by the features of their degeneration, called the "degeneration method," or sometimes from the name of the physiologist who introduced it, the "Wallerian method," has proved of great utility. Thus in the vagus nerve which is composed not only of fibres which spring from the real vagus root but also of fibres proceeding from the spinal accessory roots, the two may be distinguished by section of the vagus and spinal accessory roots respectively. We shall presently see that this method may be applied to the differentiation of tracts of fibres in the brain and spinal cord.

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SEC. 2. THE STRUCTURE OF THE SPINAL CORD.

§ **562**. Lying within the vertebral canal the spinal cord is protected by its 'membranes,' the dura mater, the arachnoid membrane and the pia mater. The consideration of the arrangement of these membranes and of the structure of the dura mater and arachnoid we will leave until we come to speak of the vascular and lymphatic supplies of the central nervous system; the histology of the pia mater may more fitly come with that of the spinal cord itself.

Along its whole length from its junction with the bulb to its termination in the *filum terminale* the spinal cord, while possessing certain general features, is continually changing as to special features. It will be convenient to study first the general structure of some particular part, for instance the middle of the thoracic (dorsal)[1] region, and afterwards to point out the special features which obtain in the several regions.

A transverse vertical section of either a fresh or a hardened and prepared spinal cord at the thoracic region possesses an outline which is roughly speaking circular. In the middle of the anterior or ventral surface is a vertical fissure, *the ventral* or *anterior fissure* (Fig. 96, *A. F.*) running some way across the thickness of the cord from the ventral towards the dorsal surface. Opposite to it on the posterior or dorsal surface is a corresponding, deeper but narrower, *dorsal* or *posterior fissure* (Fig. 96, *P. F.*) which, however, as we shall see, differs materially in nature from the

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[1] It is very desirable to use the terms 'dorsal' and 'ventral' for the parts of the cerebro-spinal axis which lie respectively near the dorsal or back part, and the ventral or belly part of the body, instead of the terms posterior and anterior; but if this is done, the use of the word dorsal to denote the region of the cord between the lumbar and cervical regions is apt to lead to confusion; hence the introduction of the word thoracic. If this use of dorsal and ventral be adhered to, before and behind, above and below, may conveniently be used to denote nearer the head and nearer the tail (or coccyx) respectively; anterior and posterior may also be used in the same sense except in the case of anterior and posterior fissure and horn, which terms seem too much honoured by time to be thrown aside.

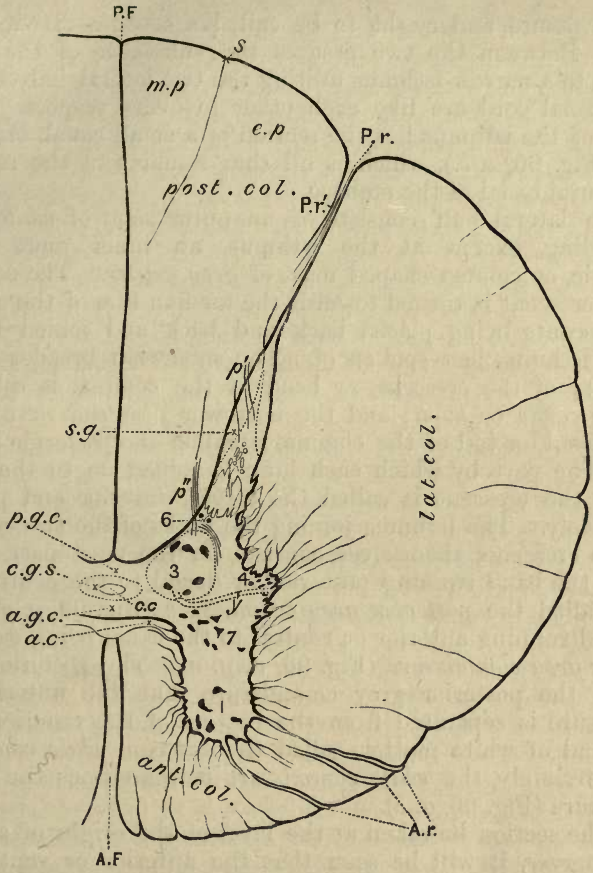

FIG. 96. A TRANSVERSE DORSOVENTRAL SECTION OF THE SPINAL CORD (HUMAN) AT THE LEVEL OF THE SIXTH THORACIC (DORSAL) NERVE. (Sherrington)[1].

Magnified 15 times. One lateral half only is shewn. The large conspicuous nerve-cells (drawn from actual specimens) are shaded black to render their relative size, shape and position more obvious; the outline of the grey matter has been made thick and dark in order to render it conspicuous.

A.F. anterior fissure. *P.F.* posterior fissure. *c.c.* central canal. *c.g.s.* central gelatinous substance. *A.r.* anterior root, *P.r.* lateral (or intermediate) bundle, *P.r'.* median bundle of posterior root of spinal nerve, *p'*, *p''* fibres of posterior root passing *p'*, indirectly through the substance of Rolando, *p''*, directly into grey matter. *a.g.c.* anterior grey commissure. *p.g.c.* posterior grey commissure. *a.c.* anterior white commissure. *ant. col.* anterior column. *lat. col.* lateral column. *post. col.* posterior column. *s.g.* the substance of Rolando. *s.* septum marking out the external posterior column or column of Burdach, *e.p.* from the median posterior column or column of Goll, *m.p.*

1. cells of the anterior horn. 3. posterior vesicular column or vesicular cylinder, or column of Clarke; the area of the cylinder is defined by a dotted line. 4. cells of the intermedio-lateral tract or lateral horn. 6. cells of the posterior horn. 7. cells of the anterior cervix. *y* a tract of fibres passing from the vesicular cylinder to the lateral column.

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[1] For this and many succeeding figures I am deeply indebted to my friend and former pupil Dr Sherrington who has kindly prepared the figures for me from his original drawings.

anterior fissure, and ought to be called a septum rather than a fissure. Between the two fissures the substance of the cord is reduced to a narrow isthmus uniting the two lateral halves, which in a normal cord are like each other in every respect. In the middle of the isthmus lies the section of a small canal, *the central canal* (Fig. 96, *c. c.*), which is all that remains of the relatively wide neural canal of the embryo.

Each lateral half consists of an outer zone of *white matter* surrounding, except at the isthmus, an inner more or less crescentic, or comma shaped mass of *grey matter.* The convexity of each crescent is turned towards the median line of the cord, the two crescents being placed back and back and joined together by the isthmus just spoken of. The somewhat broader anterior extremity of the crescent, or head of the comma, is called the *anterior cornu* or *horn*; and the narrower posterior extremity of the crescent, or tail of the comma, is called the *posterior cornu* or *horn.* The part by which each horn is joined on to the middle part of the crescent is called the *cervix*, anterior and posterior respectively. The isthmus joining the backs of the two crescents, like the crescents themselves, consists, for the most part, of grey matter, the band running posterior or dorsal to the central canal being called the *posterior grey commissure* (Fig. 96, *p. g. c*), and the band running anterior or ventral to the canal being called the *anterior grey commissure* (Fig. 96, *a. g. c*). The posterior fissure touches the posterior grey commissure, but the anterior grey commissure is separated from the bottom of the anterior fissure by a band of white matter, called the *anterior white commissure* or, more simply, the *white commissure* or sometimes the *anterior commissure* (Fig. 96, *a. c*).

If the section be taken at the level of the origin of a pair of spinal nerves, it will be seen that the anterior or ventral root, piercing the white matter opposite the head of the comma in several distinct bundles (Fig. 96, *A.r*), plunges into the anterior cornu, while the posterior or dorsal root (Fig. 96, *P.r*, *P.r′*), having the appearance of a single undivided bundle, passes, in part at least, into the posterior horn. Both roots are dispersed lengthways along the cord, the hinder roots of one nerve being close to the foremost roots of the nerve below, but it is only the anterior roots which are dispersed sideways. The compact bundle of the posterior root divides, with tolerable sharpness, the white matter in each lateral half of the cord into a posterior portion lying between the posterior fissure and the posterior root (Fig. 96 *post. col.*), which portion since, as we shall see, it runs, in the form of a column along the length of the cord, is called the *posterior column*, and into a portion lying to the outside of the posterior root between it and the anterior fissure, called the *antero-lateral column.* This latter may be considered as further divided, by the entrance of the anterior roots into a *lateral column* (Fig. 96, *lat. col.*) between the posterior root and the most external bundle of the anterior root, and into an *anterior column* (Fig. 96, *ant. col.*) between the anterior fissure and the most external bundle of the anterior root. The part traversed by the bundles of the anterior root, as they make for the anterior horn, accordingly belongs to the anterior column; but some writers speak of the anterior column as lying between the anterior fissure and the nearest bundle of the anterior root, thus making the region of the anterior root belong to neither anterior nor lateral column. And indeed the distinction between the anterior and the lateral column is to a great extent an artificial distinction.

§ **563**. The 'white matter' consists exclusively of medullated fibres supported partly by connective tissue and partly by a peculiar tissue known as *neuroglia*, of which we shall presently speak. The fibres are of various sizes, but many of them are large, and in all of them the medulla is conspicuous. They run for the most part longitudinally, so that in transverse sections of the cord nearly the whole of the white matter appears under the microscope to be composed of minute circles, the transverse sections of the longitudinally disposed fibres, imbedded in the supporting structures. The 'grey matter' also contains medullated fibres, but these are for the most part exceedingly fine fibres possessing a medulla which appears to differ from that of an ordinary nerve-fibre, since it does not stain readily with osmic acid, but is rendered visible by special modes of preparation such as that known as Weigert's. Hence these fine fibres are not apparent in ordinary carmine or other specimens, and indeed their presence was for a long time overlooked. Besides these fine medullated fibres, if we may call them such, the grey matter contains, what the white matter does not, nerve-cells with branching processes, naked axis-cylinders, and delicate filaments arising from the division of axis-cylinders or from the branching of nerve-cells, all these various structures being imbedded in neuroglia. Owing to the relative abundance of the white refractive medulla, the white matter possesses in fresh specimens a characteristic opaque white colour; hence the name. The grey matter from the relative scantiness of medulla has no such opaque whiteness, is much more translucent, and in fresh specimens has a grey or rather pinky grey colour, the reddish tint being due to the presence partly of pigment and partly of blood, for the blood vessels are much more abundant in the grey matter than in the white.

The pia mater which closely invests the cord all round consists of connective tissue, fairly rich in elastic elements and abundantly supplied with blood vessels; it is indeed essentially a vascular membrane and furnishes the nervous elements of the cord with their chief supply of blood. It sends in at intervals partitions or septa of the same nature as itself radiating towards the central grey matter. The narrow posterior fissure is completely filled up by a large septum of this kind, indeed as we have said is in reality not a fissure but a large septum; but the anterior fissure is too wide for such an arrangement; the whole membrane dips down into this fissure, following the surface of the cord and being reflected at the bottom. From these primary septa, secondary finer septa still composed of ordinary fibrillated connective tissue, carrying blood vessels, branch off; but these are soon merged into the peculiar supporting tissue called, as we have said, neuroglia. This consists in the first place of small branching cells, lying in various planes. The branching is excessive, so that the body of the cell is reduced to very small dimensions, indeed at times almost obliterated, the nucleus disappearing while the numerous branches are continued as long fine filaments or fibres pursuing a devious but for the most part a longitudinal course. In the second place these cells and fibres or filaments are imbedded in a homogeneous ground substance. Relatively to the fibres and ground substance the bodies of the cells (which are called Deiter's cells), especially bodies such as bear obvious nuclei, are very scanty; hence in sections, especially in transverse sections, of the cord the neuroglia has often a dotted or punctated appearance, the dots being the transverse sections of the fine longitudinally disposed fibres imbedded in the ground substance. Examined chemically the neuroglia is found to be composed not like connective tissue of gelatine, but of a substance which appears to be closely allied to keratin, the chief constituent of horny epidermis, hairs and the like, § 435, and which has therefore been called *neurokeratin*, (see also § 68). And indeed this neuroglia, though like connective tissue a supporting structure, is not, like connective tissue, of mesoblastic, but of epiblastic origin. The walls of the neural canal of the embryo which are transformed into the spinal cord of the adult consist at first of epithelial, epiblastic cells; and while some of these cells become nervous elements, others become neuroglia. The epithelial cells which are destined to form neuroglia become exceedingly branched, while their originally protoplasmic cell-substance becomes transformed to a large extent into neurokeratin.

The neuroglia fills up the spaces between the radiating larger septal prolongations of the pia mater and the finer branched septa which starting from the larger ones carry minute blood vessels into the interior of the white matter. In these spaces it is so arranged as to form delicate tubular canals, of very variable size, running for the most part in a longitudinal direction. Each of these tubular canals is occupied by and wholly filled up with a medullated nerve-fibre of corresponding size. A medullated nerve-fibre of the white matter of the spinal cord resembles a medullated nerve-fibre of a nerve (§ 68) in being composed of an axis-cylinder and a medulla; but it possesses no primitive sheath or neurilemma. This is absent and indeed is not wanted; the tubular sheath of neuroglia affords in the spinal cord (and as we shall see in the central nervous system generally) the support which in a nerve is afforded by the neurilemma. Nodes are, according to most authors, absent, but some say they are present.

The white matter of the cord consists then of a more or less solid mass of neuroglia, having the structure just described, which is permeated by minute canals, some exceedingly fine and carrying very fine 2μ fibres, others larger and carrying fibres up to the size of 15μ. This mass is further broken up into areas by the smaller and larger vascular connective tissue septa with the edges and endings of which the neuroglia is continuous. Most of the nerve-fibres, as we have said, run longitudinally and in a transverse section of the cord are cut transversely; but as we shall see fibres are continually passing into and out of the white matter, and in so doing take a more or less transverse course; these however are few compared with those which run in a longitudinal direction. On the outside of the cord below the pia mater the neuroglia is developed into a layer of some thickness from which nerve fibres are absent; this is often spoken of as an inner layer of the pia mater; but being neuroglia and not connective tissue is of a different nature from the pia mater proper. A layer of this superficial neuroglia also accompanies the larger septa, and a considerable quantity is present in the large septum called the posterior fissure.

The pia mater carries not only blood vessels but also lymphatics; of these however we shall speak when we come to deal with the vascular arrangements of the whole of the central nervous system.

§ **564.** In the grey matter we may distinguish the larger, more conspicuous nerve-cells and the rest of the grey matter in which these cells lie. We have already (§ 99) described the general features of these larger nerve-cells, and shall have presently to speak of their special characters and grouping. Meanwhile the most important point to remember about them besides the fact that they vary largely in form and size is that while one process may or does become an axis cylinder of a nerve-fibre, the others rapidly branch, and breaking up into fine nerve filaments are lost to view in the rest of the grey matter.

These larger nerve-cells form, however, a part only, and in most regions of the cord the smaller part, of the whole grey matter. In a transverse section from the thoracic region (Fig. 96) a few only of these larger nerve-cells are seen in the whole section, and though they appear more numerous in sections from the cervical and especially from the lumbar regions (Figs. 98, 99), yet in all cases they occupy the smaller part of the area of the grey matter. The larger part of the grey matter consists, besides a neuroglia supporting the nervous elements, of nerve filaments running in various directions and forming, not a plexus properly so called, but an interlacement of extreme complexity. These filaments are, on the one hand, the fine medullated fibres spoken of above as being recognized with difficulty, and, on the other hand, non-medullated filaments ranging from fairly wide and conspicuous naked axis-cylinders down to fibrils of extreme tenuity, the latter arising apparently either from the division of axis-cylinders of nerve fibres passing into or out of the grey matter or from the continued branching of processes of nerve cells. By the modes of preparation now available it has been shewn that the fine medullated fibres so far from being rare, are in certain parts of the grey matter so abundant as even to preponderate over the non-medullated fibres or fibrils. Lastly, besides the conspicuous nerve cells spoken of above, which, though of various sizes, may all perhaps be spoken of as large, a very large number of other cells of small size, some of which at all events must be regarded as true nerve-cells, are present in the grey matter.

The neuroglia in which all these structures, nerve-cells, fine medullated nerve-fibres, naked axis-cylinders and fine filaments, are imbedded is identical in its general characters with that of the white matter, but, as naturally follows from the nature of the nervous elements which it supports, is differently arranged. Instead of forming a system of tubular channels it takes on the form of a sponge work with large spaces for the larger nerve-cells and fine passages for the nervous filaments. At the junction of the grey matter with the white matter, the neuroglia of the one is continuous with that of the other, and the connective tissue septa of the latter run right into the former; the outline of the grey matter is not smooth and even, but broken by tooth-like processes due to the septa. Since, as we have just said, some of the true nerve-cells are very small, and since the nerve filaments like the neuroglia fibres are very fine and take like them an irregular course, it often becomes very difficult in a section to determine exactly which is neuroglia and which are nervous elements. The neuroglia cells may however be distinguished perhaps from the smaller nerve-cells by their nuclei not being so conspicuous or so relatively large as in a nerve-cell, and by their staining differently.

The grey matter then may be broadly described as a bed of neuroglia, containing a certain number of branching nerve-cells, for the most part though not exclusively large and conspicuous, but chiefly occupied by what is not so much a plexus as an intricate interweaving of nerve filaments running apparently in all directions. Some of these filaments are fairly conspicuous naked axis-cylinders, and a few are easily recognized medullated fibres of ordinary size; but by far the greater number are either exceedingly fine medullated fibres, whose medulla is only made evident by special modes of preparation or delicate fibrils devoid of medulla. With the nervous web formed by these filaments the branching processes of the nerve-cells, on the one hand, and the divisions of nerve-fibres passing into or out of the grey matter, on the other hand, appear to be continuous. It may be added that the grey matter is well supplied with blood vessels, these being in it, as stated above, relatively much more numerous than in the white matter.

§ **565.** The central canal is lined by a single layer of columnar epithelial cells, which are generally described as bearing cilia; but it is not certain that the processes which may be seen projecting from the surfaces of the cells are really cilia. These epithelial cells rest not on a distinct basement membrane but on a bed of neuroglia, free apparently or nearly so from nervous elements, which surrounds the central canal and is sometimes spoken of as the *substantia gelatinosa centralis* (Fig. 96, *c. g. s.*). The attached bases of the epithelial cells are branched or taper to a filament, and become continuous with the branched cells or fibres of the neuroglia below. As we said above the neuroglia elements are transformed epithelial cells; and the continuity of the cells, which retaining the characters of epithelial cells form a lining to the canal, with the cells which have become branched and lost their epithelial characters indicates the epithelial origin of the latter.

The central canal with the surrounding area of neuroglia forms the central part of the isthmus uniting the two lateral halves of the cord. Posterior (dorsal) to this central mass lies the *posterior grey commissure* (Figs. 96, 98, 99, *p. g. c.*), composed chiefly of fine filaments running transversely, and anterior (ventral) to it lies first the thinner *anterior grey commissure* (Figs. 96, 98, 99, *a. g. c.*) of a similar nature, and then the relatively thick *white commissure* (Figs. 96, 98, 99, *a. c.*) which is formed by medullated fibres crossing over from one side of the cord to the other, and thus constitutes a decussation of fibres along the whole length of the cord. On each side, the central mass of neuroglia of which we are speaking gradually merges into the central grey matter of the corresponding lateral half.

The end or head (caput) as it is frequently called of the posterior horn is occupied not by ordinary grey matter, but by a peculiar tissue, the *substantia gelatinosa of Rolando*, which forms a sort of cap to the more ordinary grey matter but differs in size and shape in different regions of the cord. Cf. figs 96, 97, 98, *s.g.* In carmine and some other modes of preparation it is frequently stained more deeply than is the ordinary grey matter, and in such preparations is very conspicuous. It may be described as consisting of a somewhat peculiar neuroglia traversed by fibres of the posterior root, and containing a large number of cells, which, for the most part small, the cell-bodies being small relatively to the nuclei, are not all alike, some being probably nervous and others not. It takes origin from the cells forming the immediate walls of the embryonic medullary canal. In the embryo, this canal is relatively wide, though compressed from side to side, and in transverse sections of the medullary tube appears at a certain stage as a narrow oval slit placed vertically, and reaching almost from the dorsal to the ventral surface. The dorsal part of this long slit is later on closed up by the coming together of the walls and the obliteration of the greater part of the cavity, leaving the ventral part to form a circular canal, which by the development of the anterior columns assumes the central position. During this closure of the dorsal part of the canal a mass of the cells lining the canal is cut from the rest on each side, and during the subsequent growth takes up a position at the end of the posterior horn. Hence, though it never apparently contains any cavity, the substance of Rolando may be regarded as an isolated portion of the walls of the medullary canal, which has undergone a development somewhat different from that of the portion which remains as the lining of the central canal. Traces of this origin may be seen even in the adult. Thus in the lower end of the cord, in what we shall speak of presently as the *conus medullaris*, the central canal widens out dorsally, and in section (Fig. 97, *A*) presents on each side a bay *x*, stretching out towards the position of the posterior horn. At this region of the cord, though both white and grey matter are developed on the ventral surface, the posterior columns do not meet on the dorsal surface, but leave the central canal covered only by tissue which perhaps may be called neuroglia, but is of peculiar nature and origin. In the calf, in a part of the dorsal region the substance of Rolando is not confined to the tip of the posterior horn, but is continued to meet its fellow in the middle line. Fig. 97, *B*. If we imagine the dorsal portion of the canal of *A* to be cut off from the ventral portion, its cavity to be obliterated, and the lining epithelium with some of the surrounding elements to undergo a special development, the condition

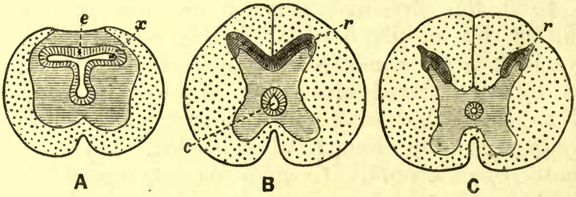


Fig. 97. Diagram to illustrate the nature of the Substance of Rolando.

The figures are purely diagrammatic and are not drawn to the same scale. In all three figures the grey matter is shaded with fine lines and the white matter with dots.

A. transverse section of the lower end of the conus medullaris in man. *e*. epithelium lining the medullary canal. *x*. lateral expansion of the canal.

B. transverse section of the spinal cord of the calf in the lower thoracic region. *r*. substance of Rolando. *c*. central canal.

C. transverse section through mid thoracic region of cord in man.

in *B* is reached by the growth of the posterior columns. From *B*, the transition to the normal state of things as in 97, *c*, is a very slight one. The extreme dorsal tip of the horn being of a more open texture than the substance of Rolando, is sometimes called the *zona spongiosa*.

§ **566**. *The grouping of the nerve-cells.* The nerve-cells, at all events the cells which are large enough to be easily and without doubt recognized to be nerve-cells, form, as we have seen, only a part of the grey matter, and in some parts of the cord, in the thoracic region for instance, are so sparse that in a section of the spinal cord in this region thin enough to shew its histological features satisfactorily, the bodies of a few only of such cells are visible (Fig. 96); the greater part of the grey matter consists not of the bodies of conspicuous nerve-cells, but of a mass of fibres and fibrils passing apparently in all directions. In the cervical (Fig. 98) and especially in the lumbar (Fig. 99) regions the nerve-cells are both absolutely and relatively more abundant; but even in a section taken from the lumbar region the nerve-cells, all put together, form the smaller part of the whole area of grey matter. Moreover, in respect of the number of cells all the sections of even the same region of the cord are not alike. Seeing that the cord may be considered as growing out of the fusion of a series of paired ganglia, each ganglion corresponding to a nerve, cf. § 96, we may fairly expect to find the fusion not complete, so that the nerve-cells would appear more numerous opposite a nerve than in the middle between two nerves. In some of the lower animals this arrangement is most obvious, and there are some reasons for thinking that even in man the nerve-cells are metamerically increased at the level of each nerve.

Even when casually observed it is obvious that the nerve-cells are not scattered in a wholly irregular manner throughout the grey matter, being for instance much more conspicuous in the anterior horn than elsewhere; and more careful observation allows us to arrange them to a certain extent in groups.

The cells of the anterior horn are for the most part large and conspicuous, $67\,\mu$ to $135\,\mu$ in diameter, branch out in various directions, and present an irregular outline in sections taken in different planes. We have reason to think that every one of them possesses an axis-cylinder process which, in the case at all events of most of the cells, passing out of the grey matter becomes a fibre of the adjacent anterior root. They are obvious and conspicuous in all regions of the cord, though much more numerous and individually larger in the cervical and lumbar enlargements than in the thoracic region. We may further, with greater or less success, divide them into separate groups.

In the cervical and lumbar regions a fairly distinct group of cells is seen lying on the median side of the grey matter close to the anterior column (Figs. 98, 99, 1). This may be called *the*

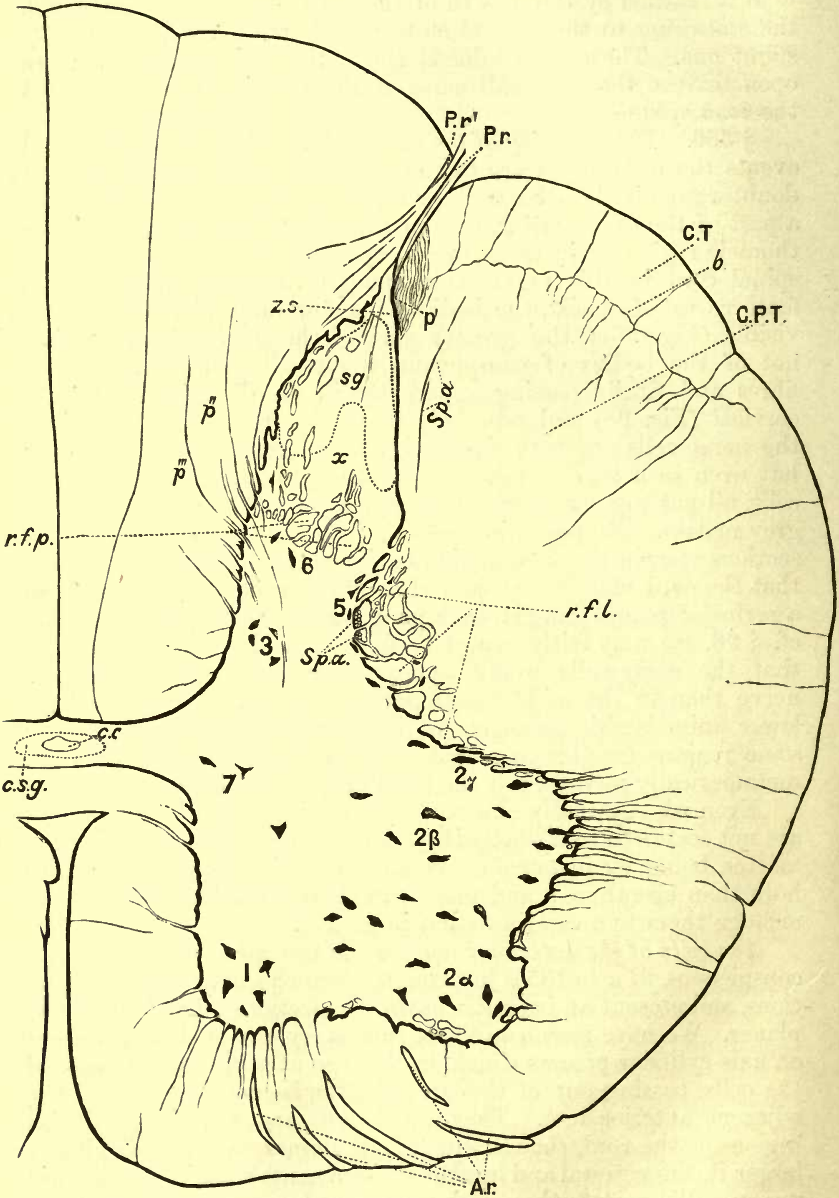

P.r'
P.r.
C.T
b
C.P.T.
z.s.
p'
sg
Sp.a
p''
p'''
x
r.f.p.
6
5
r.f.l.
3
Sp.a.
c.c
c.s.g.
7
2γ
2β
1
2α
A.r.

Fig. 98. Transverse Dorsoventral Section of Spinal Cord (Human) at the Level of the Sixth Cervical Nerve. (Sherrington.)

This is drawn on the same scale as Fig. 96, that is magnified 15 times.

r. f. l. lateral reticular formation. *r. f. p.* posterior reticular formation. p'. fine fibres of lateral bundle of the posterior root; p'', p''' fibres of median bundle of posterior root, entering grey matter from external posterior column. *x.* grey matter of posterior horn. *Sp. a.* bundles of fibres belonging to the spinal accessory nerve; in the lateral reticular formation they are seen cut transversely. *b.* is a natural septum of connective-tissue marking out the cerebellar tract *C. T.* from the crossed pyramidal tract *C. P. T.* *z. s.* zona spongiosa. 2 *a*, β, γ, lateral cells of the anterior horn. 5. Cells in the region of the lateral reticular formation. The other letters of reference are the same as in Fig. 96.

median group. It appears also in the thoracic region (Fig. 96, **1**); indeed the question arises whether all the cells of the anterior horn in this region do not belong to this group. The other cells so conspicuous in the lumbar and cervical enlargements, and therefore probably in some way associated with the limbs, may be spoken of as forming altogether a *lateral group*; but we may, though with some uncertainty, subdivide them into two or three groups. Thus in the lumbar region a group of cells (Fig. 99, **2**γ) lying near the lateral margin of the more dorsal part or base of the horn may be distinguished, as a *lateral subgroup*, from the cells occupying the ventral lateral corner of the horn and forming a *ventral* or *anterior subgroup* (Fig. 99, **2***a*); and the same distinction, though with less success, may be made in the cervical region (Fig. 98). Further, we may perhaps in both regions distinguish a group of cells placed more in the very middle of the horn as a *central subgroup* (Figs. 98, 99, **2**β). But, in all cases, the separation of these cells, which we have spoken of as a whole as lateral cells, into minor groups, is far less distinct than the separation of the median group from these lateral cells, especially if we admit that in the thoracic region, the median group is alone clearly represented.

In the thoracic region a group of rather smaller cells is seen at the base of the anterior horn, near to the junction with the isthmus (Fig. 96, **7**). In the cervical and lumbar region these cells are very scanty (Figs. 98, 99, **7**).

The cells of the posterior horn contrast strongly with those of the anterior horn in being few, and for the most part small. They are branched; and though we have reason to believe that, like the cells of the anterior horn, they possess each an axis-cylinder process, this is not easily determined by actual observation; the processes do not run out to join the posterior root as do the corresponding processes in the anterior horn and therefore are not so readily seen. These cells occur in all regions of the cord, and appear to be arranged into two more groups. The lateral margin of the posterior horn, at about the middle or neck of the horn, is along the whole length of the cord, but especially in the cervical region, much broken up by bundles of fibres passing in various directions and forming an open network, called the *lateral reticular formation* (Fig. 98, 99, *r. f. lat.*). In all regions of the cord a number of cells are found associated with this reticular formation, forming *the group of the lateral reticular formation* (Figs. 98, 99, **5**). In all regions of the cord also a group of cells (Figs. 96, 98, 99, **6**) is found in that part of the horn where, a little ventral to the substance of Rolando, the uniform field of grey matter is broken up into a kind of network by a number of bundles of white fibres running in various directions. This network has also been called a

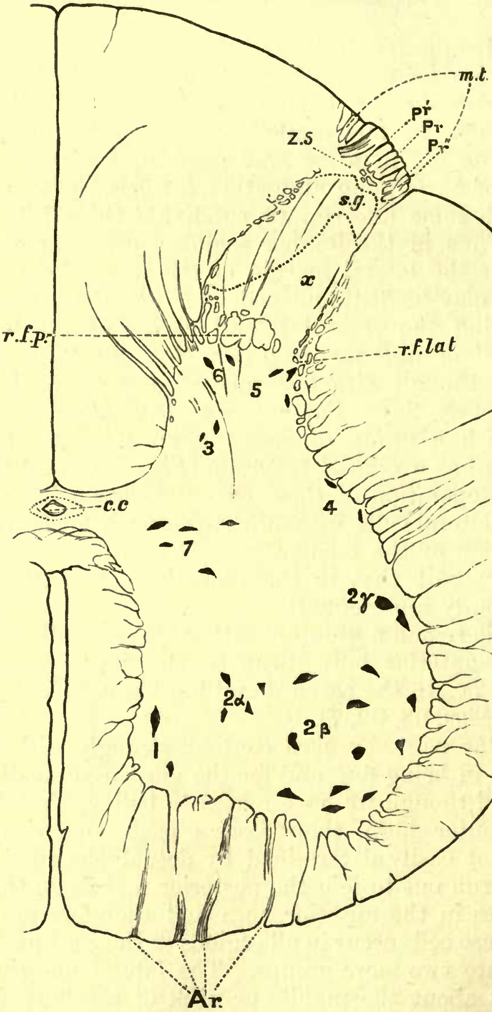


Fig. 99. Transverse Dorsoventral Section of the Spinal Cord (Human) at the Level of the Third Lumbar Nerve. (Sherrington.)

This is drawn to the same scale as Figs. 96, 97 and in the same way except that the outline of the grey matter is not exaggerated. *Pr′*. median, *Pr*. intermediate, *Pr″*. lateral bundles of posterior roots. The region comprised under *m.t.* is the marginal zone or Lissauer's zone. The other letters of reference are the same as in 96 and 98.

The three figures 96, 98, 99 are intended to illustrate the main differential features of the cervical, thoracic, and lumbar cord.

reticular formation, and has received the name of *posterior reticular formation* (Figs. 98, 99, *r. f. p.*) to distinguish it from the lateral reticular formation just mentioned; the two however in some regions (see Fig. 96) join each other, and thus cut off a ventral portion of the posterior horn containing nerve-cells from a dorsal portion, x in Figs. 98, 99, in which no obvious or conspicuous nerve-cells are present.

The groups of cells just mentioned with the restrictions and modifications spoken of occur along the whole length of the cord; but the group of cells to which we must now call attention is almost confined to a special region of the cord, or at least is but feebly represented elsewhere. In the thoracic region, especially in the lower thoracic region (we shall return to the limits of the group later on) at the base of the posterior horn (Fig. 96, **3**) just ventral to the curve formed by the posterior grey commissure as this bends dorsally to join the posterior horn, is seen on each side of the cord a conspicuous group of cells known as *Clarke's column* or the *posterior vesicular column* or *vesicular cylinder*. The cells composing this group, though varying in size at different levels, are rather large cells, and are for the most part fusiform, with their long axis placed lengthways along the cord, so that in transverse sections they often appear to have a rather small round body. They are surrounded by and as it were imbedded in a mass of fine fibres, the area of which is indicated by a dotted line in Fig. 96.

Also conspicuous in the thoracic region is another group of cells lying on the outer side of the middle of the grey matter at about the junction of the anterior and posterior horns. This is known as the *intermedio-lateral tract* and is sometimes called the *lateral horn* (Fig. 96, **4**). The cells composing it are somewhat small spindleshaped cells with their long axis placed transversely. The group is conspicuous as we have said in the thoracic regions; it may be recognized in the lumbar region (Fig. 98, **4**), but in the cervical region becomes confused with the most dorsally placed or lateral subgroup of the anterior horn. We shall however have to return to these groups of cells when we come to speak of the differences between the several regions of the cord.

§ **567.** *The tracts of white matter.* At first sight the white matter of the cord appears to be of uniform nature. We can use the nerve roots to delimitate the anterior, posterior and lateral columns, but we appear to have no criteria to distinguish parts in each column. In the cervical and upper thoracic regions of the cord, a septum (Fig. 96, *s.*) in the posterior column, somewhat more conspicuous than the other septa, has enabled anatomists to distinguish an inner median portion, the *median posterior column*, commonly called the *postero-median column* or *column of Goll* (Fig. 96, *m. p.*), from an outer lateral portion, the *external posterior column*, commonly called the *postero-external column* or *column of Burdach* (Fig. 96, *e.p.*), the lateral part of which, nearer the grey matter, has, for reasons which we shall see later on, been called the *posterior root-zone.* But beyond this neither the irregular septa nor other features will enable us to distinguish one part of the white matter as different in nature from another. Nor have we better success when with the scalpel we attempt to unravel out the white matter into separate strands. Nevertheless we have convincing evidence that the white matter is arranged in strands, or tracts, or columns, which have different connections at their respective ends, which behave differently under different circumstances, which we have every reason to believe carry out different functions, but which cannot be separated by the scalpel because each of them is more or less mixed with fibres of a different nature and origin. The evidence for the existence of these tracts is twofold.

One kind of evidence is embryological in nature. When a nerve fibre is being formed in the embryo, either in the spinal cord or elsewhere, the essential axis cylinder is formed first and the less essential medulla is formed later. Now when the developmental history of the spinal cord is studied it is found that, in the several regions of the cord, all the fibres of the white matter do not put on the medulla at the same time. On the contrary, in certain tracts, the medulla of the fibres makes its appearance early, in others later. By this method it becomes possible to distinguish certain tracts from others.

Another kind of evidence is supplied by facts relating to the degeneration of the fibres of the white matter. We have seen (§ 561) that the degeneration of a nerve fibre is the result of the separation of the fibre from its trophic centre, and that while the trophic centre of the afferent fibres is in the ganglion on the posterior root, that of the efferent fibres is in some part of the spinal cord. In the case of the efferent fibres the degeneration might be spoken of as *descending* from the spinal cord to the muscles or other peripheral organs. In the case of the afferent fibres of the trunk of the nerve, the degeneration is also one descending from the ganglion down to the skin or other peripheral organ. When however the section is carried through the posterior root of a spinal nerve, the degeneration takes place in the part of the nerve between the section and the spinal cord, it runs up from the section to and into the spinal cord, and may therefore be called an *ascending* degeneration. Thus we may say that when a nerve trunk or when a nerve root is cut completely across, all the fibres which are thereby separated from their trophic centres, degenerate. When the nerve trunk is divided all the fibres below the section undergo descending degeneration. If the anterior root be cut across, all the fibres of the root below the section undergo descending degeneration. If the posterior root be cut across, all the fibres of the root above the section undergo ascending degeneration with the exception of certain fibres which do not degenerate at all, and of which we shall speak later on.

When the spinal cord is cut across, for instance in the dorsal region, all the fibres of the white matter do not degenerate either in the part of the cord above the section or in the part below. Some fibres, and indeed some tracts of fibres degenerate, and some do not. Further, some tracts degenerate in the cord above the section, and thus undergo what has been called an ascending degeneration; other tracts degenerate in the cord below the section, and thus undergo what has been called a descending degeneration. These terms must however be used with caution. When a nerve trunk is cut across, the degeneration actually descends, in the sense that the progress of the degenerative changes may be traced downwards; they begin at the section and travel downwards at a rate sufficiently slow to permit a difference being observed between the progress of degeneration at a spot near the section and that at one farther off. After section of or injury to the spinal cord, however, it is not possible to trace any such progress either upwards or downwards; in the tracts both above and below the section or injury, degeneration either begins simultaneously along the whole length of the degenerating tract, or progresses along the tract so rapidly that no differences can be observed as far as the stage of degeneration is concerned between parts near to and those far from the section or injury. When, for instance, the cord is divided in the cervical region, subsequent examination of the tracts of so-called descending degeneration shews that the degeneration is as far advanced in the lumbar region far away from the section as in the cervical region just below the section. Applied to the spinal cord, therefore, the term descending degeneration means simply degeneration below the seat of injury or disease, ascending degeneration means simply degeneration above the seat of injury or disease. We may add that the histological features of the degeneration of fibres in the spinal cord are not wholly identical with those of the degeneration of fibres in a nerve trunk. Thus, the neurilemma with its nuclei being absent from the fibres of the cord, no proliferation of nuclei takes place; the axis-cylinder and medulla simply break up, are absorbed and disappear.

Similar degenerations, ascending, or descending or both, are seen when the section is not carried right through the whole cord, but particular parts of the cord are cut through or simply injured. And similar degenerations occur as the consequences of disease set up in parts of the cord.

In this way the results of sections of or of other injuries to or of diseases of the spinal cord have enabled us to mark out certain tracts of the white matter as undergoing degeneration and others as not, and moreover certain tracts as undergoing descending and others as undergoing ascending degeneration. Further, the delimitation of tracts of white matter by the process of degeneration agrees so well with the results of the embryological method as to leave no doubt that the white matter does consist of tracts which differ from each other in nature and in function.

The several tracts thus indicated vary in different regions of the cord. They may be broadly described as follows.

I. *Descending Tracts,* that is to say, tracts which undergo a descending degeneration in the sense noted above.

The most important and conspicuous is a large tract (Fig. 100, *cr. P.*) occupying the posterior part of the lateral column, coming close upon the outer margin of the posterior horn, and for the most part not reaching the surface of the cord. We shall have to return to this tract more than once, and may here simply say that it is most distinctly marked out by both the embryological and the degeneration methods, that it may be traced along the whole length of the cord from the top of the cervical region to the end of the sacral region, and that it enters the cord from

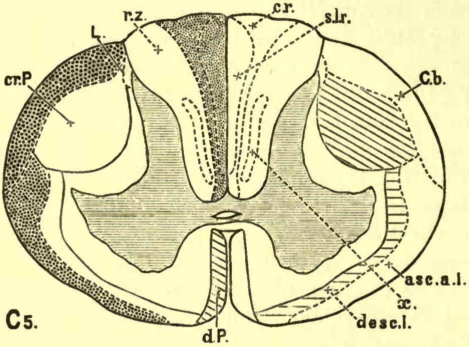


FIG. 100. DIAGRAM TO ILLUSTRATE THE GENERAL ARRANGEMENT OF THE SEVERAL TRACTS OF WHITE MATTER IN THE SPINAL CORD. (Sherrington.)

The section is taken at the level of the fifth cervical nerve. The relations of the tracts in different regions of the cord are shewn in Fig. 104.

The ascending tracts, tracts of ascending degeneration, are shaded with dots, the descending tracts, tracts of descending degeneration, are shaded with lines; the shading is in each case put on one side of the cord only the reference letters being placed on the other side.

cr.P. crossed pyramidal tract, or more shortly pyramidal tract. *d.P.* direct pyramidal tract, shaded on the side opposite to that on which *cr.P.* is shaded, in order to indicate the difference of the two as to crossing. *C.b.* cerebellar tract. *s.lr.* and *cr.* together indicate the median posterior tract or tract of fibres of the posterior roots, *cr.* representing, as is explained more fully in the text, the cervical and *s.lr.* the sacral, lumbar and dorsal roots. *asc.a.l.* the antero-lateral ascending tract. *desc.l.* the antero-lateral descending tract. The area, not shaded, marked *x*, is the small descending tract or rather patch mentioned in the text as observed, in certain regions of the cord, in the external posterior column *rz.* The small area at the tip of the posterior horn, marked L, is the posterior marginal zone or Lissauer's zone.

the brain through the structures called the pyramids of the bulb, which we shall study later on. These pyramids cross over or decussate as they are about to pass into the cord, forming what is known as the decussation of the pyramids, and the tract of fibres in question shares in this decussation. Hence this tract is called the *crossed pyramidal tract* or more simply the *pyramidal tract*.

A smaller, less conspicuous descending tract occupies the median portion of the anterior column (Fig. 100, *d. P.*) This is not only much smaller but also much more variable than the crossed pyramidal tract, is not present in the lower animals, being found in man and the monkey only and being better developed in man than in the monkey, and reaches a certain way only down the spinal cord, generally coming to an end in the thoracic region. It too comes down from the pyramid, and is a continuation of that part of the pyramid which unlike the rest does not decussate in the bulb; thus the tract which coming down from the left side of the brain runs in the left pyramid in the bulb, passes down into the left anterior column of the cord. Hence this smaller tract is called the *direct pyramidal tract*.

These two are the most conspicuous and important descending tracts, but names have been given to two other descending tracts. One, known as the *antero-lateral descending tract*, is a large tract placed in the antero-lateral column, and seen in section (Fig. 100, *desc. l.*) as an elongated area stretching from the pyramidal tract towards the anterior column and reaching at times as far as the anterior fissure. The area is large, however, because the tract is very diffuse, that is to say, the fibres with descending degeneration, or fibres which degenerate below the section or injury, are very largely mixed up with fibres which do not degenerate; in this respect this tract contrasts with the pyramidal tract, which is to a much greater extent composed of fibres with descending degeneration, though even in it there are a considerable number of fibres which do not degenerate. Indeed this antero-lateral descending tract is so diffuse that it hardly deserves to be called a tract.

The other is a small, narrow, comma-shaped tract (Fig. 100, *x*), situated in the middle of the external posterior column which has been observed in the cervical and upper thoracic regions, and has been called the "descending comma tract." But the degeneration reaches a short way only, below the section or injury, and the group of fibres thus degenerating can hardly be considered as forming a tract comparable to the other tracts. The area probably represents fibres of the posterior root which take a *descending* course soon after their entrance into the cord.

II. *Ascending tracts*, that is to say, tracts in which the degeneration takes place above the section or injury.

A conspicuous ascending tract of a curved shape (Fig. 100, *C. b.*) occupies the outer dorsal part of the lateral column lying to the outside of the crossed pyramidal tract, between it and the surface of the cord. It appears to begin in the upper lumbar region, being said to be absent from the lower lumbar and sacral cord, and may be traced upwards increasing in size through the thoracic and cervical cord to the bulb. In the bulb it may be traced into the restiform body or inferior peduncle of the cerebellum, and so to the cerebellum; for the restiform body serves, as we shall see, in each lateral half of the brain, as the main connection of the cerebellum with the bulb and spinal cord. Hence this tract is called *the cerebellar tract.*

A second important ascending tract occupies the median portion of the posterior columns (Fig. 100, *cr.*, *s.lr.*), and so far coincides with what we described above as the median posterior column, in the upper regions of the cord, that it may be called the *median posterior tract;* it extends along the whole length of the spinal cord, varying at different levels in a manner which we shall presently study, and ending above in the bulb.

A third ascending tract, called the *ascending antero-lateral tract,* or tract of Gowers, occupies (Fig. 100, *asc. a. l.*) the outer ventral part of the lateral column. It has somewhat the form of a comma, with the head filling up the angle left between projecting portions of the cerebellar and pyramidal tracts, and the tail stretching away ventrally along the outer margin of the lateral column outside the antero-lateral descending column, the end of the tail often reaching to the anterior roots. It may be traced along the whole length of the cord, but is not so distinct and compact a tract as the two ascending tracts just mentioned; the fibres with ascending degeneration, that is to say the fibres degenerating above the section or seat of injury, are very largely mixed with fibres of a different nature and origin.

We may further remark that these several tracts differ from each other, in some cases markedly, as to the diameter of their constituent fibres. Thus the cerebellar tract is composed almost exclusively of remarkably coarse fibres. The median posterior tract, on the contrary, is made up of fine fibres of very equable size, while the fibres of the antero-lateral ascending tract are of a size intermediate between the other two. The pyramidal tract on the other hand is made up of fibres of almost all sizes mixed together.

The tracts then which are thus marked out are, as descending tracts, the crossed and the direct pyramidal tracts, with the less distinct or important antero-lateral descending tract: and, as ascending tracts, the cerebellar tract, the median posterior tract and the less distinct antero-lateral ascending tract. If we suppose all these tracts taken away there is still left a considerable area of white matter, namely, nearly the whole of the external posterior column, the external anterior column, including the region traversed by the bundles of the anterior roots, and that part of the lateral column which lies between the antero-lateral descending tract and the crossed pyramidal tract on the outside and the grey matter on the inside. From this area of white matter we may put on one side at present the external posterior column because, as we shall see, this column is largely composed of the fibres of the posterior root which pass through this column, especially through the lateral part of it near the grey matter, on their way to their ultimate destination; hence the alternative name of posterior root-zone. We may similarly leave for the present the small zone of white matter composed of very fine fibres known as *the posterior marginal zone* or Lissauer's zone (Fig. 100, *L.*), lying dorsal to the tip of the posterior horn and in the lower regions reaching to the outside of the cord; for this too belongs to the fibres of the posterior root. Leaving these parts out of consideration we may say as regards the rest of the white matter, that the present state of our knowledge will not allow us to divide it into special tracts. All this area is largely composed of fibres which do not undergo either ascending or descending degeneration as the result of section, injury or disease. It has been suggested that these fibres either have no trophic centre at all or have double ones, one above and one below, on either of which they can in case of need lean; so that when the fibre is divided at any level, the upper portion is still nourished from some centre above, and the lower from some centre below. At all events, whether this be the true explanation or no, the fibres in this part of the white matter cannot be differentiated into tracts by a study of their degeneration. Fibres of this kind, which we can speak of neither as ascending nor as descending, also occur in the external posterior column mingled with the fibres of the posterior root. And we may repeat the caution, that even in the several ascending and descending tracts just described, especially in those which we spoke of as less distinct or as more diffuse, many fibres are present which undergo neither ascending nor descending degeneration.

§ **568.** It may be as well perhaps to insist here once more, that when these several tracts or the fibres running in the tracts are spoken of as ascending or descending, what is meant is that the degeneration takes place above the section or seat of injury or disease in the one case, and takes place below in the other. It has been supposed by many that the nervous impulses which these fibres severally carry, travel in the same direction as that taken by the degeneration, that the ascending tracts carry impulses from below upward, that is to say, carry impulses which arising from peripheral organs pass to various parts of the spinal cord or of the brain, that they are, in other words, channels of afferent impulses, and that conversely the descending tracts carry efferent impulses. To this view is often added as a corollary, that the tracts which do not degenerate at all carry impulses both ways, and hence cannot be considered as either afferent or efferent channels but simply as communicating channels. Upon this it may be remarked that impulses do not necessarily travel in the same direction as the degeneration; when a spinal nerve trunk is divided the afferent fibres as well as the efferent fibres both degenerate in a descending direction towards the periphery, though the former carry impulses in the other direction. Hence the direction of degeneration is no proof of the direction in which impulses travel; moreover, as we have seen, degeneration does not actually travel along the fibres of the spinal cord in the same way that it does along the fibres of a nerve trunk. It may be that the descending tracts do carry impulses in a descending direction, that is, efferent impulses, and that the ascending tracts serve to carry afferent impulses; but the proof that they do thus respectively act must be supplied from other facts than those of degeneration. Moreover, we shall have to return to these ascending and descending tracts and to study their behaviour along the length of the cord before we can use the facts concerning them as a basis for any discussion as to their functions.

§ 569. *The connections of the nerve roots.* If we regard the spinal cord, and apparently we have right to do so, as resulting from the fusion of a series of segments or metameres, each segment, represented by a pair of spinal nerves, being a ganglionic mass, that is to say a mass containing nerve-cells with which nerve fibres are connected, we should expect to find that the fibres of a spinal nerve soon after entering in, or before issuing from the spinal cord are connected with nerve-cells lying in the neighbourhood of the attachment of the nerve to the cord. We should, we say, expect to find this; but owing to the difficulty of tracing individual nerve fibres through the tangled mass of the substance of the cord, our actual knowledge of the termination of the fibres of the posterior root, and origin of the fibres of the anterior root is at present far from complete.

With regard to the *anterior root,* there can be no doubt that a very large proportion of the fibres in the root are continuations of the axis-cylinders of cells in the anterior horn. The fibres which can thus be traced are of large diameter and appear to be chiefly if not exclusively motor fibres for the skeletal muscles. In the frog a laborious enumeration on the one hand of the number of fibres in the anterior roots, and on the other hand of the number of cells of the anterior horn in the areas corresponding to the nerve roots has, it is true, shewn a very remarkable agreement in number between the two. We might be inclined from this to conclude that all the fibres of an anterior root start directly from cells in the anterior horn, and that all the cells in the anterior horn end in fibres of the nearest anterior root. But several considerations prevent us from trusting too much to this observation, especially in the case of the higher animals. The anterior root contains other fibres than motor fibres for the skeletal muscles, vaso-motor fibres for instance, secretory fibres and others; and it is *a priori* unlikely that these should have origin from the same cells as the motor fibres of the skeletal muscles. Moreover, as a matter of fact some of the fibres have been traced through the anterior horn, on the one hand towards the posterior horn and on the other hand towards the lateral column; others again are found to pass through the anterior horn of their own side to the bottom of the anterior fissure where, crossing over to the other side and thus forming part of the anterior white commissure, they appear to ascend to the anterior horn of the other side. We cannot at present make any positive statement as to the real origin and exact nature of these fibres which thus upon entering the cord pass by the cells in the anterior horn without joining them, though those which cross by the anterior white commissure are supposed to take origin in the cells of the anterior horn of the other side; it is sufficient for our present purposes to remember that while a large number of the fibres of the anterior root, presumably those supplying the skeletal muscles, take origin in the cells of the anterior horn, shortly before they issue from the cord, others have some other origin. And similarly we have reason to think that all the cells in the anterior horn do not send out axis-cylinder processes to join the anterior roots of the same side. We may however regard a large number at all events of the cells of the anterior horn, at the level of as well as a little below and a little above the level of the exit of any particular anterior root, as constituting a sort of nucleus of origin for the larger number of the fibres, and those most probably the skeletal motor fibres, of that anterior root.

The *posterior root* enters the cord not in several bundles laterally scattered as does the anterior root, but in a more compact mass. This mass however consists of at least two distinct bundles, which upon their entrance into the cord, take different courses. One bundle, the larger one, lying to the inner or median side of the other, consisting of relatively coarse fibres, and called the *median bundle* (Fig. 98, *Pr′*), passes obliquely into the lateral part of the external posterior column, which, as we have said, is in consequence often spoken of as the posterior root-zone. Here the fibres changing their direction run longitudinally for some distance upwards (some however, certainly in the upper cervical region, and probably in other regions, run a short distance downwards) but eventually either go, as we shall see, to form the median posterior tract or make their way back into the grey matter at the base of the posterior horn and thus join the vesicular cylinder, though some are said to be continued on through the grey matter into the anterior horn. The other smaller bundle placed to the outside of the former, and called the *lateral bundle* (Fig. 98, *Pr*), may be again divided into an *intermediate bundle* (Fig. 99, *Pr*) lying next to the median bundle, and into a still more lateral bundle (Fig. 99, *Pr''*). The former, consisting also of coarse fibres, plunges directly through the substance of Rolando at the extremity of, and so into the grey matter of the horn, where the fibres changing their direction run in part at least longitudinally in the grey matter in bundles known as "the longitudinal bundles of the posterior horn" Figs. 98, 99 *r. f. p.* some of which appear to pass on to the anterior horn. The small most external or lateral portion of the lateral bundle, consisting of fine fibres and sometimes spoken of as *the* lateral bundle, on entering the cord at once ascends for some distance, and thus forms the thin layer of fine fibres, the posterior marginal zone or Lissauer's zone, indicated in Fig. 99 by *m. t.*, which lies between the actual extremity of the horn and the surface of the cord, and in the upper regions of the cord (cf. Fig. 98, *p'*) runs some way upward on the lateral margin of the horn between the grey matter and the crossed pyramidal tract. As it ascends this layer continually gives off fibres to the grey matter of the posterior horn in the cells of which they appear to end.

Thus, while part of the median bundle does not join the grey matter at all but goes to form the median posterior tract, the rest of that bundle and all the other fibres of the root, sooner or later, join the grey matter either of the posterior horn or of some other part.

§ **570**. *The Special Features of the several regions of the Spinal Cord.* The cord begins below in the slender filament called the *filum terminale,* which lying in the vertebral canal, in the midst of the mass of nerve roots called the *cauda equina,* rapidly enlarges at about the level of the first lumbar vertebra into the *conus medullaris.* This may be regarded as the beginning of the lower portion of a fusiform enlargement of the cord known as the *lumbar swelling,* which reaches as high as about the attachment of the roots of the twelfth or eleventh thoracic nerve at the level of the eighth thoracic vertebra, the broadest part of the swelling being about opposite the third lumbar nerve. Above the lumbar swelling, through the thoracic region the somewhat narrowed cord retains about the same diameter until it reaches the level of the first or second thoracic nerve opposite the seventh cervical vertebra where a second fusiform enlargement, the *cervical swelling,* broader and longer than the lumbar swelling, begins. The broadest part of the cervical swelling is about opposite to the fifth or sixth cervical nerve; from thence the diameter of the cord becomes gradually somewhat less until it begins to expand into the bulb, but even in the highest part is greater than in the thoracic region. The sectional area of the cord increases therefore from below upwards, but not regularly, the irregularity being due to the lumbar and cervical swellings.

The extremity of the filum terminale is said to consist entirely of neuroglia closely invested by the membranes, even the central canal being absent. A little higher up the central canal begins, and nerve-cells with nerve-fibres make their appearance in the neuroglia; thus a kind of grey matter covered by a thin superficial layer of white matter is established. We have already referred to the peculiar features of the lower end of the conus § 565; but higher up the canal becomes central and small, the posterior columns are developed, and the grey matter contains more nervous elements and relatively less neuroglia, becomes in fact ordinary grey matter. From thence onward to very near the junction with the bulb, where transitional features begin to come in, the spinal cord may be said to have the general structure previously described.

The sectional area of the white matter increases in absolute size and on the whole in a steady manner from below upwards. In other words, in a section at any level, the number of longitudinal fibres forming the white matter is greater than the number at a lower level, and less than the number at a higher level; for any difference which may exist in the diameter of the individual fibres is insufficient to explain the differences in the total sectional area of the white matter. If we were to measure in man the sectional area of each of the spinal nerves as it joins the cord, and to add them together, passing along the cord from below upwards the results put in the form of a curve would give us some such figure as that shewn in Fig. 101; the area gained by adding together the sectional areas of the nerves increases in a fairly steady manner from below upwards. The curve of the sectional area of the white matter of the cord taken from below upwards would be very similar, but if anything more regular. It must be understood however that the dimensions of the areas would not be the same in the two cases. The sectional area of the white matter at the top of the cervical region, though greater than any where lower down, is far less than the united sectional area of all the nerves below that level. The white

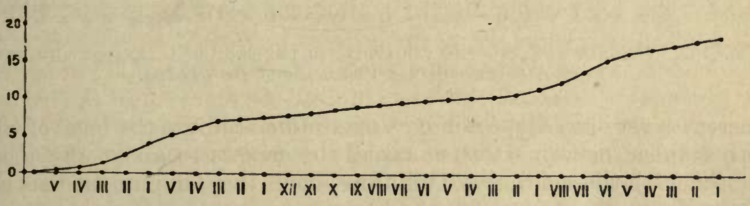


Fig. 101. Diagram shewing the united sectional areas of the Spinal Nerves, proceeding from below upwards.

In this as in the succeeding figures 102—3, —5, —6, —7, all of which refer to man, the left hand side represents the bottom of the cord and the right hand the top of the cord, the numerals indicating successively the sacral, lumbar, thoracic and cervical nerves. The several figures are not drawn to the same scale.

matter is not formed by all the fibres from the nerves which join the spinal cord continuing to run along the cord up to the brain; as we have seen, some at least of the fibres end in the grey matter. Nevertheless the white matter in passing up the cord appears to receive a permanent addition at the entrance of each nerve. We may infer that each nerve has a representative of itself starting from the level of its entrance and running up to some part of the brain. Whether the fibres thus representative of the nerve are continuations of the very fibres of the nerve itself, or are new fibres starting from some relay of grey matter, with which the fibres of the nerve are also connected, is another question.

§ **571.** The grey matter in contrast to the white matter shews great variations in area along the length of the cord (Fig. 102). From the entrance of the coccygeal nerve upwards the area increases very rapidly, reaching a maximum at about the level of the 5th lumbar nerve. It then rapidly decreases to about the level of the 11th thoracic nerve, maintains about the same dimensions all through the thoracic region, and begins to increase again at about the level of the 2nd thoracic nerve. Its second maximum is reached at about the level of the 5th or 6th cervical nerve, after which the area again becomes smaller, remaining however at the upper cervical region much larger than in the thoracic region.

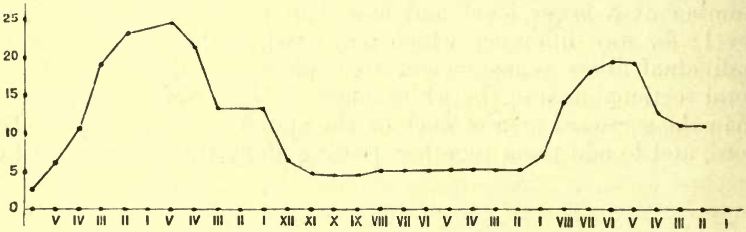


Fig. 102. Diagram shewing the variations in the sectional area of the grey matter of the Spinal Cord, along its length.

The meaning of these variations becomes clear when we turn to Fig. 103, which shews in a similar diagrammatic manner the sectional areas of the several spinal nerves. It will be observed that the increase and decrease of the sectional area of the grey matter follow very closely the increase and decrease of the quantity

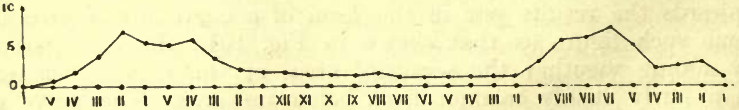


Fig. 103. Diagram shewing the relative sectional areas of the Spinal Nerves, as they join the Spinal Cord.

of nerve, that is to say, neglecting differences in the diameter of the fibres, in the number of nerve-fibres passing into the cord. The sectional areas of the 1st and 2nd sacral, 4th and 5th lumbar nerves are very large, and opposite to these the sectional area of the grey matter of the cord is very large also; the enlargement of grey matter which is the essential cause of the lumbar swelling is correlated to the large number of fibres which enter and leave the cord at this region to supply chiefly the lower limbs. Similarly the enlargement of grey matter which is the essential cause of the cervical swelling is correlated to the large number of fibres which enter and leave this region of the cord to supply chiefly the upper limbs. In the thoracic region, where the number of fibres entering and leaving the cord is relatively less, the sectional area of the grey matter is also less. Since the attachments of the several spinal nerves are not exactly equidistant from each other along the length of the cord, the sectional area is not an exact measure of bulk; the total bulk of grey matter for instance belonging to two nerves which enter the cord close together is less than that of two nerves giving rise to the same sectional area of grey matter as the former two but entering the cord far apart from each other. Still the error which may be introduced by taking sectional area to mean bulk is, for present purposes at all events, so small that we may permit ourselves to say that in the successive regions of the spinal cord the bulk of grey matter in any segment is greater or less according to the size of the nerve (or pair of nerves, right and left) belonging to that segment.

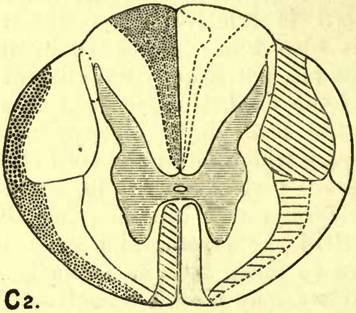
From this anatomical fact we appear justified in drawing the conclusion that at all events a great deal of the grey matter of the spinal cord may be considered as furnishing a nervous mechanism, with which the efferent fibres of each spinal nerve just before they leave the cord, and the afferent fibres soon after they join the cord are more immediately connected. It may be that the whole of the grey matter is thus directly connected with and thus rises and falls with the fibres of the nerves; or it may be that there is a sort of core of grey matter, which maintains a uniform bulk along the whole length of the cord and serves as a basis which is here more and there less swollen by the addition of the grey matter more immediately connected with the fibres of the nerves. This question the method which we are now using cannot settle.

§ **572.** Owing to these different rates of increase of the grey and white matter respectively along the length of the cord, we find that in sections of the cord taken at different levels the appearances presented vary in a very distinct manner. This is strikingly shewn by comparing Figs. 96, 98 and 99. At the level of the third lumbar nerve (Fig. 99) the grey matter is very large, reaching as we have seen, its maximal sectional area at about this point, so that although the area of white matter is not very great the whole area of the cord is considerable.

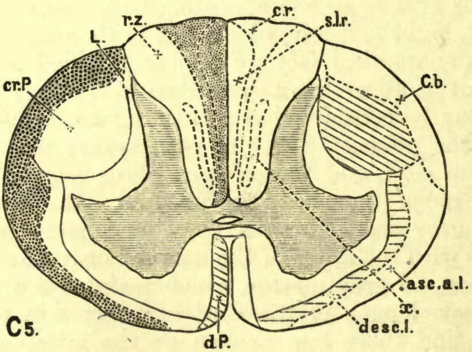
At the level of the sixth thoracic nerve (Fig. 96), in spite of the white matter having very decidedly increased, the grey matter has shrunk to such very small dimensions, that the total sectional area of the cord has markedly diminished.

At the level of the sixth cervical (Fig. 98) the grey matter has again increased, reaching here as we have seen its second maximum; the white matter has also further increased, and that indeed very considerably, so that the total area of the cord is much greater than in any of the lower regions.

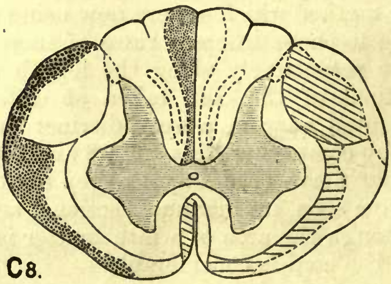
Further details of the varying size of the white matter and of the grey matter at different levels are also shewn in the series given



C2.



C5.



C8.

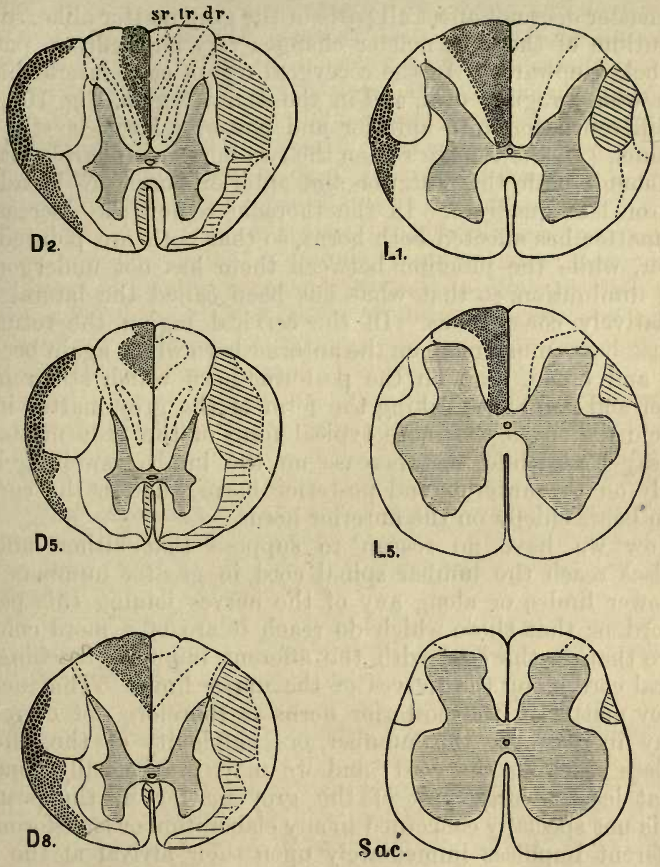


Fig. 104. Diagram illustrating some of the features of the Spinal Cord at different levels. (Sherrington.)

All the figures are drawn to scale, and represent the cord magnified four times. They shew the differences at different levels in the shape and size of the cord, in the outline of the grey matter, and in the relative position of the anterior and posterior fissures, and also shew the variations at different levels of the several 'tracts' of the white matter.

C_2 at the level of the second cervical nerve, C_5 of the fifth cervical, C_8 of the eighth cervical. D_2 of the second thoracic, D_5 of the fifth thoracic, L_1 of the first lumbar, L_5 of the fifth lumbar, and Sac. of the second sacral nerve.

The shading of the tracts is the same as in Fig. 100; but in the median posterior column of D_2 the areas of fibres coming from the sacral nerves *s. r.*, and lumbar nerves *l. r.* are distinguished from the area, *d. r.* of fibres belonging to the thoracic nerves. In C 8, no distinction is made between any of these sets of fibres; in L 5 only fibres of sacral nerves are represented; in L_1 D_8 D_5, the more dorsal small portion corresponds to sacral fibres and the next to lumbar, or lumbar thoracic nerves.

in Fig. 104. In these, combined with the three figures just referred to, it will be observed that the serial increase and decrease of the grey matter does not affect all parts of the grey matter alike, so that the outline of the grey matter changes very markedly in passing from below upwards. In the coccygeal region each lateral half is a somewhat irregular oval, and in the sacral region, Fig. 104, *Sac*, the differentiation into anterior and posterior horns is still very indistinct. In the lumbar region the two horns are sharply marked out, though both the posterior and anterior horns are broad and more or less quadrate. In the thoracic region the decrease of grey matter has affected both horns, so that both are pointed and slender, while the junction between them has not undergone so much diminution, so that what has been called the lateral horn is relatively conspicuous. In the cervical region the returning increase bears much more on the anterior horn which again becomes large and broad, than on the posterior horn which still remains slender and pointed. Taking the form of the grey matter in the thoracic region as the more typical form of the grey matter we may say that while the increase on the lumbar swelling bears equally on the anterior and posterior horns, that in the cervical region bears chiefly on the anterior horns.

Now we have no reason to suppose that either afferent impulses reach the lumbar spinal cord in greater numbers from the lower limbs, or along any of the nerves joining this part of the cord, or that those which do reach it are of a more complex nature than is the case with the afferent impulses reaching the cervical cord along the nerves of the upper limbs. The increase of grey matter in the posterior horns is therefore not correlated to any increase in the number or complexity of the afferent impulses reaching the cord; and we may, provisionally conclude that at least a large part of the grey matter in the posterior horn is not specially concerned in any elaboration or transformation of afferent impulses immediately upon their arrival at the cord. Indeed we have seen that while there is ample evidence to connect the nerve cells, and therefore presumably the grey matter in general of the anterior horn with the efferent motor fibres of the anterior root, there is no corresponding evidence as to any large immediate connection of the afferent fibres of the posterior root with the nerve cells or indeed any other part of the grey matter of the posterior horn. We may add that, as we shall point out later on, so essential is the concurrence of appropriate afferent impulses to the due carrying-out of complex coordinate motor or efferent impulses, that we can scarcely expect to find any increase in the nervous mechanisms devoted to the purely motor function of carrying out motor impulses without a corresponding increase in the nervous mechanisms belonging to the afferent impulses, by means of which those motor impulses are guided and coordinated. Hence, were the latter nervous mechanisms restricted to the posterior horns we should expect to find a greater parallelism than does actually exist between them and the anterior horns.

§ **573**. The changes in the area of grey matter illustrated by the statements and diagrams given above refer to the grey matter as a whole, that is, not only to nerve cells, but also to strands and networks of nerve fibres and nerve fibrils, and indeed include to a certain extent neuroglia. We have seen § 566 that we are able to distinguish certain large and conspicuous nerve cells in the grey matter and to arrange these into groups. The grey matter contains many other small nerve cells, which we are not able at present to name or arrange, but whose existence must always be borne in mind. Confining ourselves now however to the groups of larger, more conspicuous nerve cells, we find that, broadly speaking, the chief differences which can be observed in the cells of the anterior horn along the length of the cord are that in the thoracic region the nerve cells of the anterior horn are few, and relatively small, while in the cervical and lumbar region, especially in the latter, they are numerous and large. It is not easy, even if possible, to distinguish in the thoracic region the several groups of cells marked in Figs. 98, 99 as **2**α, β, γ; the median group (Figs. 98, 99, **1**), indeed seems to be the only group present in the mid thoracic region (Fig. 96, **1**). The group of the posterior horn (Figs. 96, 98, 99, **6**) appears to be about the same in all regions.

With two other groups of nerve cells striking differences are seen in different regions. The vesicular cylinder, for instance (Fig. 96, **3**), is most conspicuous in the thoracic region. It may be said to reach from the 7th or 8th cervical nerve to the 3rd lumbar nerve, being perhaps most developed in the lower thoracic and upper lumbar region. It is absent in the cervical region above the 7th or 8th cervical nerve, and in the lumbar region below the 3rd lumbar nerve; but a similar group of cells is present opposite the 2nd and 3rd cervical nerves; a group of more doubtful likeness is seen in the sacral region below; and the column is said to have a representative in the bulb above the spinal cord proper. It seems natural to infer that the cells forming this vesicular cylinder are connected neither with the ordinary somatic motor fibres governing the skeletal muscles, nor with the ordinary afferent sensory, somatic fibres coming from the skin and elsewhere, but in some way with some special sets of fibres; on this point however no authoritative statement can as yet be made.

The lateral horn or intermedio-lateral tract Fig. 96, **4** is also most conspicuous in the thoracic region. In the lumbar region, it is lost or traced with great difficulty, and in the cervical region seems to be merged into the most dorsally placed division of the lateral group of the cells of the anterior horn. It is possible that this group represents in the limbless thoracic region the cells which are developed into the great lateral group of the anterior horn in the regions of the limbs.

§ **574.** The white matter as we have seen increases in sectional area with considerable regularity from below upwards. If instead of a diagram of the increase of the whole white matter, we construct in a similar way diagrams of the anterior, posterior and lateral columns respectively we find that while the sectional area of the lateral column (Fig. 105) increases with some considerable regularity from below upwards, though not so regularly as does the whole area of white matter, both the anterior (Fig. 106) and the posterior (Fig. 107) columns agree to a certain extent with the grey matter in shewing a decided increase in both the lumbar and the cervical swellings. We may, provisionally at least, infer from this that, while considerable portions of both the anterior and the posterior columns are like the adjoining grey matter in some way or other concerned in the exit and entrance of efferent and afferent fibres, the larger portion of the lateral column is concerned in the transmission of impulses to and fro, between the local mechanisms below, immediately connected with the several spinal nerves, and the brain above. This conclusion seems incidentally

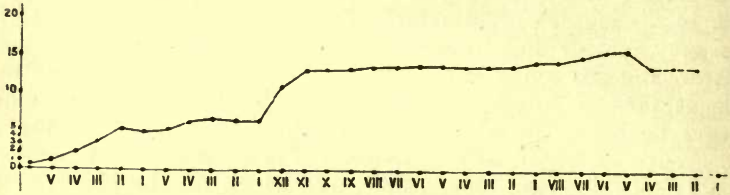


Fig. 105. Diagram shewing the variations in the sectional area of the lateral columns of the Spinal Cord, along its length.

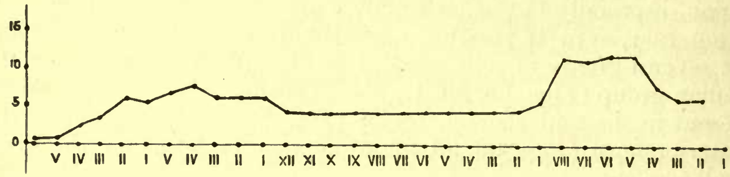


Fig. 106. Diagram shewing the variations in the sectional area of the anterior columns of the Spinal Cord, along its length.

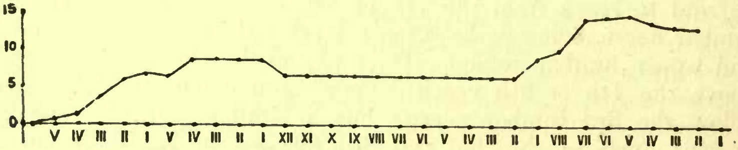


Fig. 107. Diagram shewing the variations in the sectional area of the posterior columns of the Spinal Cord, along its length.

confirmed, (though these diagrams must not be strained to carry detailed inferences,) by the sudden increase of the lateral column above the lumbar swelling, as if the large mass of nervous mechanism for the lower limbs concentrated in this region demanded a sudden increase in the number of fibres connecting it with the brain above.

This more or less continuous increase of the lateral column partly explains the change of form in the general outline of the transverse section of the cord which is observed in passing upwards from the lower to the higher regions. In the coccygeal, sacral and lumbar regions the outline, though varying somewhat chiefly owing to the disposition of the grey matter, is on the whole circular. In the thoracic region especially in the upper part the increase of the lateral columns increases the side to side diameter so much that the section becomes oval, and in the cervical region this increase of the side to side diameter out of proportion to the dorso-ventral diameter is very marked. The actual outline of the whole transverse section is however determined also to a certain extent by the changes of form of the grey matter.

The cord moreover undergoes along its length a change which is not very clearly indicated in the diagrams Figs. 106, 107. By comparing the series of transverse sections given in Fig. 104 it will be seen that the relative position of the central canal shifts along the length of the cord. In the sacral and lumbar regions the central canal is nearly at the centre of the circle of outline, and the posterior and anterior fissures are nearly of equal depth. Even in the upper lumbar region, and still more in the thoracic region the position of the central canal is shifted nearer to the ventral surface so that the posterior fissure becomes relatively longer, deeper, than the anterior. This shifting goes on through the cervical region up to about the level of the 2nd cervical nerve, where it is arrested by the beginning of the changes through which the spinal cord is transformed into the far more complicated bulb.

This lengthening of the posterior fissure indicates an increase in the dorso-ventral diameter of the posterior columns, and this, not being accompanied by a compensating diminution of the side to side diameter, shews in turn that the posterior columns undergo an increase in passing upwards. From this we may add to the provisional conclusion just arrived at with regard to the lateral columns, the further conclusion that some part of the posterior columns also is concerned in transmitting impulses, in a more or less direct manner, between the various regions of the cord below and the brain above. The anterior columns do not increase in the same marked manner, though over and above the increase due to the lumbar and cervical swellings, a continued increase may be observed especially in the upper cervical region; it is in this upper region that the direct pyramidal tract is best developed.

§ 575. The provisional conclusions at which we have arrived are further, to a certain extent at least, confirmed and extended by a study of the behaviour at the several regions of the cord of the special tracts of white matter described in § 567.

The pyramidal tract, that is to say, the crossed pyramidal tract entering the spinal cord above from the pyramid is very large in the cervical region, having the form and situation shewn in Fig. 104, $C_2C_5C_8$. From thence downward it diminishes in size, the diminution being especially rapid in the lumbar swelling, Fig. 104, L_1, where the tract being no longer covered in by the cerebellar tract comes to the surface of the cord; but it may be traced by the degeneration method down as far as the coccygeal region, and indeed appears to be coexistent with the entrance of spinal nerves into the cord. Diminution of the tract means a lessening of the number of fibres; and since we cannot suppose that any of the fibres come suddenly to an end in the tract itself we are led to infer that along the cord, from above downwards, fibres are successively leaving the tract and passing to some other part of the cord. We seem further justified in concluding that the fibres which thus successively leave the tract go to join the series of local nervous mechanisms with which the spinal nerves communicate, as we have seen reason to believe, upon their entrance into the cord. Indeed, as we shall see later on, we have reason to think that the nervous mechanisms which the fibres in question join are those belonging to the motor fibres of the anterior roots. This pyramidal tract does not begin in the pyramid, but may be traced through the lower parts of the brain right up to special areas in the cortex or surface of the cerebral hemispheres; and very strong reasons may be brought forward in support of the view that the fibres of this tract are fibres which carry impulses from the cortex to successive portions of the spinal cord, and there give rise to efferent impulses which pass to appropriate skeletal muscles. The tract, therefore, is not only a descending tract by virtue of the mode of degeneration, but may be spoken of in a broad sense as a tract of efferent impulses descending from the cerebral cortex; and indeed it is maintained that it is the channel of the particular kind of efferent impulses which we shall speak of as voluntary or volitional impulses. We may add that as the tract passes along a path which we shall subsequently describe, from the cerebral cortex through the lower parts of the brain to the pyramid, it gives off fibres to mechanisms connected with several of the cranial nerves, much in the same way that it gives off fibres to the spinal nerves.

We may therefore picture to ourselves this pyramidal tract as starting in the form of a broad sheaf of fibres from a certain district on the surface of one of the cerebral hemispheres. Putting aside for the present any possible increase of the number of fibres by division of fibres (though we have reason to think that this does to a certain extent occur) we may regard the tract as being at its maximum at its beginning in the cortex. As it descends to the decussation of the pyramids in the bulb it loses a certain number of fibres, which pass off to the cranial nerves. Having crossed and entered into the lateral column of the cord it continues to give off fibres to the spinal nerves, probably to the anterior root of each in succession, and so goes on its way down the cord continually diminishing until the last remaining fibres are given off to the last coccygeal nerve.

When degeneration is set up along this tract, as may be done, by injuries to particular areas of the cerebral cortex, the main mass of degenerated fibres, after crossing over from one side of the cerebrospinal axis to the other in the decussation of the pyramids at the lower end of the bulb, during its further progress down the spinal cord, keeps to the side to which it has crossed right down to the end. Hence, as we have said, it is called the crossed pyramidal tract. The main mass of fibres, the degeneration of which has been started by injury to the left side of the brain crosses over to the right side of the spinal cord and runs down the lateral column of the right side to the end of the cord. Nevertheless some fibres appear to cross over again in the spinal cord and then to run along the same side as the side of the brain injured; along the left side in the case just mentioned. Such fibres are spoken of as "recrossed fibres."

The direct pyramidal tract (Fig. 104, *dP*), except that it does not cross at the decussation of the pyramids is otherwise similar to the crossed pyramidal tract, and indeed is a part of the same strand to which the crossed tract belongs. When degeneration in this tract is started by injury to particular areas of the cerebral cortex, say on the left half of the brain, the degeneration may be traced through the left anterior pyramid, and so to the left median anterior column of the spinal cord. The direct tract is never so extensive or marked as the crossed tract, does not reach so far down, is much more variable both in length and in sectional area and, as we have said, is almost confined to man. Diminishing as it descends it may be said to cease in the middle thoracic region Fig. 104, D_5D_8. Taking an average we may say that, of the whole strand running in the pyramids above the decussation, about three-fourths of the fibres go to form the crossed and about one-fourth to form the direct tract. We shall see later on that the impulses coming down along the united tract in the brain, may broadly speaking, be said to cross over wholly from one side to the other before they reach the skeletal muscles, so that the impulses passing along fibres in, say, the left pyramid, reach the muscles of the right limbs and right side of the body whether the fibres cross over at the decussation to form the crossed or remain on the same side to form the direct pyramidal tract. We are therefore led to infer that the fibres in the direct tract, as they pass down the cord, cross over in the cord itself before they make connections with the fibres of the anterior roots. Probably the crossing is effected by means of some of the decussating fibres which form the anterior white commissure. A part only, indeed a small part, of the commissure can serve this purpose; most of the fibres of the commissure, and in the lower regions of the cord, where the direct tract no longer exists, all the fibres must have some other functions. Some of the fibres of this great pyramidal tract, leave the tract, as we have said, to join some of the cranial nerves before the pyramids of the bulb are reached; and the impulses passing along these fibres also cross over to the opposite side before they issue along the cranial nerves. Hence we infer that these fibres decussate above the decussation of the pyramids just as those of the direct tract decussate below it. So that of the whole strand as it leaves the cerebral cortex, while the main mass of fibres crosses over at the decussation of the pyramids, the rest of the fibres cross the middle line in succession from the level of the third cranial nerve to the level of the lower limit of the direct tract; below the decussation of the pyramids the crossing takes place by means of the anterior commissure of the cord, above the decussation by means of what we shall later on learn to speak of as the raphe of the bulb, or by structures corresponding to this higher up.

§ 576. The *cerebellar tract* (Fig. 104, *Cb*) is as we have seen a tract of ascending degeneration; the degeneration in it makes its appearance above the section or the seat of other injury of the cord. It begins somewhat suddenly at the level of the second lumbar nerve region, being absent at least as a distinct tract below; injury of the cord at the level of the middle and lower lumbar nerves leads to no marked tract of degeneration (though possibly scattered single fibres may degenerate), while injury higher up does. The tract lies, as we have said, close to the surface of the cord in the posterior part of the lateral column just outside the crossed pyramidal tract, and while varying somewhat in the shape of its section from level to level remains throughout a somewhat narrow crescentic patch. At the top of the spinal cord it passes, as we have said, from the lateral columns into the restiform bodies of the bulb, and so to certain parts of the cerebellum.

When the section or lesion is limited to one side of the cord, the degeneration is similarly limited to the same side, and that along its whole course up to the cerebellum; there is no evidence of any of the fibres decussating in the cord.

The area of the tract increases from below upward. This has been determined by the embryological method, by noting the appearance of the medulla in the fibres, as well as by comparing the extent of the degeneration following upon a section high up in the cord with that following upon a section lower down. From this we infer that the fibres composing the tract must start successively from other parts of the cord along its length, that is to say, the tract must be fed by fibres coming from other structures in the cord. On the other hand, it is found that the degenerated area following upon a section or injury diminishes as it is traced upward; when, for instance, a section is made in the mid thoracic region the area of degeneration in the tract is greater immediately above the section than it is higher up, say in the cervical region. From this we are led to infer that though the tract is successively fed along its course by fibres coming from other parts of the cord, some of the fibres entering the tract, though like their companions undergoing an ascending degeneration, do not like them continue in the tract right up to the cerebellum, but pass off to other parts of the cord on their way upward. This, however, is equivalent to saying that the tract is not a pure or homogeneous one, but consists of at least two sets of fibres, only one of which is continued on to the cerebellum and strictly deserves the name of 'cerebellar.' It may perhaps here be mentioned that while the fibres composing the tract are as a whole conspicuously coarse, large fibres, with these there are mingled, especially in the thoracic region, a number of much finer fibres; but these apparently undergo a descending not an ascending degeneration and do not therefore really belong to the tract; they may be fibres which have strayed from the pyramidal tract.

We have as yet no very clear evidence as to the origin of the fibres which compose the tract. Unlike the case of the median posterior tract of which we have next to speak, no degeneration, at least in the lumbar and thoracic regions, appears in the tract after section merely of the roots of the nerves; to produce the degeneration the cord itself must be injured. From this we may infer that the tract is not fed directly by the fibres of the posterior roots. Some observers maintain that the tract is fed by fibres coming from the vesicular cylinder and point out that both the tract and the column begin at the same level somewhat suddenly: but the want of parallelism between the course of the tract and that of the cylinder along the length of the cord, the latter being as we said conspicuous in the thoracic region while the tract steadily increases upward, is distinctly opposed to such a view. From the fact that the degeneration taking place in it is an ascending one, it is supposed that the tract is the channel for ascending, that is to say, in a broad sense, afferent impulses. And considerable interest attaches to the fact that these impulses should be carried, not to the cerebrum but to the cerebellum. Our knowledge on this point, however, is very imperfect, and what can be said in the matter had better be said later on.

§ **577.** The *median posterior* tract is the other conspicuous tract of ascending degeneration; it also is supposed to be a channel for ascending, afferent impulses; and this view is rendered almost certain by the intimate relations of the tract to the fibres of the posterior roots.

In dealing so far with the tracts of degeneration in the spinal cord we have always spoken of the degeneration as being the result of lesions of the spinal cord itself. Experiments on animals, however, and clinical experience have shewn that division or injury of the fibres of the posterior roots is followed by tracts of degeneration in the spinal cord, though no damage whatever may have been done to the substance of the cord itself. These tracts make their appearance in the median posterior columns, the exact path and limits of the degeneration differing with the different spinal nerves. The results of the division of different groups of nerves are so instructive that we may dwell upon them in detail.

If the posterior roots of two or three lumbar nerves (on one side) be divided, an examination of the cord, after an interval long enough to allow degeneration to be well established, will bring to light the following features. The divided roots will be found to have degenerated right up to their entrance into the cord. A section of the cord opposite the entrance of the lowest divided root will shew no degeneration of the cord beyond that of the bundles of fibres passing in. A little higher up degeneration will be observed in the external posterior column close to the posterior horn; and as we ascend we find that this degeneration first spreads over a large portion of the external posterior column, and then invades the median posterior column; the degeneration does not affect the whole of the median posterior column but leaves intact a small dorsal portion, roughly triangular in shape, at the angle between the fissure and the dorsal surface of the cord, as well as some portion of the more ventral part of the column nearest the grey commissure. Still a little higher up we should find that degenerated fibres had disappeared from the external portion of the external posterior column close to the grey matter, though still existing in the more median part of that column, as well as in the median posterior column to the extent just indicated. Still a little higher up the whole of the degeneration would have disappeared from the external posterior column, but the tract of degeneration in the median posterior column would remain, the extent of degeneration being dependent on the number of roots which had been divided. Lastly, by carrying the sections still higher up the cord we should be able to trace this tract in the median posterior column right up to the bulb, where it would come to an end.

If we divided some of the thoracic nerves instead of the lumbar we should obtain very similar results: a degeneration of the external posterior columns a little above the entrance of the roots, spreading across the column towards the median line, and wholly disappearing at a certain height above, accompanied by a degeneration of a part of the median posterior column, reaching from a little distance above the entrance of the divided nerve-roots right up to the bulb. This latter tract of degeneration would however not occupy the same position as that consequent upon division of the lumbar nerves; its position would be more ventral, nearer the grey commissure, and rather more lateral. Compare Fig. 104, D_2, where *lr* indicates the degeneration due to section of the lumbar nerves, and *dr* that of the thoracic nerves. If we divided some of the cervical posterior roots we should get similar results, with the difference that the tract of degeneration in the median posterior columns would occupy a position still more ventral and still more lateral (Fig. 104, C_5 *c.r.*); while if we divided the sacral nerves the tract of degeneration would be dorsal and median to the tract belonging to the lumbar nerves, and would occupy more or less of the triangle left below that tract (Fig. 104, D_2 *s.r.*). The degeneration it will be understood is in all cases confined to the same side of the cord as that of the divided roots. We may add, in order to complete the story of the effects of division of the posterior roots, that the section leads to degeneration of the marginal zone (Lissauer's tract), but this degeneration reaches for a certain distance only up the cord and then disappears. It will be remembered that this zone is fed by fibres (of fine calibre) belonging to the external or lateral bundle of the posterior roots.

These results may be interpreted as follows. The (great majority of the) fibres of the posterior root, cut off from their ganglion by the division, degenerate centripetally towards the spinal cord. We have previously seen that many of the fibres of the root pass into the external posterior column and run up in that column for some distance. The degeneration observed in this column for some distance above the entrance of the divided roots shews that the fibres run lengthways for some distance in this column, while the disappearance of the degeneration a little higher up similarly shews that the fibres eventually leave the column. The appearance of degeneration in the median posterior column shews that some of these fibres have passed into that column from the external posterior column, and the continuation of that degeneration right up to the bulb indicates that these fibres pursue an unbroken course in that column along the whole length of the cord. The area of degeneration, or more exactly the number of degenerated fibres in the continued tract of degeneration in the median posterior column is much less than that in the temporary or short tract of degeneration in the external posterior column. This shews that some only of the fibres passing into the external posterior column go on to join the median posterior column and so reach the bulb; the rest obviously take another path, and we have already seen reason to think that many of these end in the grey matter of the cord. Hence of all the fibres joining the cord in a posterior root, while some, and these we may add are chiefly fine fibres, entering the grey matter directly or passing into the posterior marginal zone, soon make such connections that the degeneration due to the section of the root spreads no farther, a large number, and these chiefly coarse fibres, before they make any such connection pass into and occupy for some length of the cord the external posterior column. We may here remark that though these fibres are spread over the greater part of this column, they do not form the whole of the column; they are mixed up with fibres of a different nature and origin. Of these fibres of the posterior root which thus run in the external posterior column while still dependent for their nutritive activity on the ganglion of the root, some, indeed the greater part, leave the tract and make such connections in the grey matter, that their degeneration ceases; others, forming the smaller part, pass into the median posterior column, and taking up a definite position in that column pursue an unbroken course to the bulb.

All the fibres therefore of the posterior roots do not end in the grey matter soon after their entrance into the cord. A representative of each root is carried right up to the bulb by means of the median posterior column; of the axis-cylinders which leave the ganglion on the root, a certain relatively small number pursue an unbroken course for some little distance through the external posterior column, and for the rest of their way through the median posterior column, along the whole length of the cord above the entrance of the root until they find an ending in the grey matter of the bulb. Further, each spinal nerve has this representative of its posterior root placed in a definite position in the posterior median column, the arrangement being such as shewn in Fig. 104, that the lower (sacral) nerves find their place in the more dorsal and median part of the column, while the nerves above are successively placed in positions more and more ventral and external.

As far as our knowledge goes at present we are led to believe that this median posterior tract is very largely made up of fibres having this origin. It affords a channel by which afferent impulses are carried straight up the cord from the nerve trunk without making connections on the way. We may repeat that the path is confined to the same side of the cord along its whole length; there is no crossing over to the other side.

In the above description we have spoken only of the results following section of the posterior roots outside the cord; but it will be understood that similar results follow upon section of or injury to or disease of the cord itself affecting the posterior columns or the bundles of the roots as they enter the cord. When such a lesion occurs there may be observed in the region of the cord above the lesion a degeneration of the external

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posterior column, reaching some little distance up, and a more limited degeneration of a part of the median posterior column stretching right up to the bulb. The position and form of the tract of the degeneration in the median posterior column will depend on the level of the lesion along the length of the cord, according as it interrupts the ascending representatives of the sacral nerves only, or of the lumbar and sacral nerves, or of the dorsal and cervical nerves as well. A complete section or hemisection of the cord will produce results corresponding to the division on both sides or on one side of all the nerves below the section.

We may add that while, according to some observers, the strand of fibres belonging to a particular root or group of roots, having once taken up its position in the median posterior column remains unchanged until it reaches the bulb; according to others it diminishes in area, some of its fibres making connections in the cord itself.

§ **578**. The *antero-lateral ascending tract* (Fig. 104, *asc. a. l.*) is less well known than either of the two preceding; it is also more diffuse, that is to say, the fibres undergoing degeneration are more largely mixed with fibres of a different nature and origin. It appears to extend down the cord to a lower level than the cerebellar tract, but its lower limit has not yet been accurately determined. Since the degeneration taking place in it is an ascending one, it has been inferred that it serves as the path for afferent, and indeed for sensory impulses. Degeneration in it is seen only after section or injury of the substance of the cord itself, not after division of the posterior roots. If, then, it is to be regarded as a channel of afferent impulses passing into it from the posterior roots, those impulses must pass into it along those fibres of the posterior root which find secondary trophic centres in some part of the grey matter; in this respect this tract resembles the cerebellar tract, and differs from the median posterior tract. The latter is the direct continuation up the cord to the bulb of such fibres as are still trusting for their nutritive activity to the cells of the ganglion on the posterior root; the fibres of both the former trust for their nutritive activity to some part of the grey matter of the cord, and presumably to the nerve-cells of that grey matter. A further resemblance between the antero-lateral ascending and cerebellar tracts must be admitted, if future researches confirm the opinion of those who hold that the former like the latter, at the top of the cord, pass along the restiform body to the cerebellum. Indeed under such a view it would appear probable that the antero-lateral tract is simply a more diffuse and outlying part of the cerebellar tract.

§ **579**. We may now briefly pass in review, somewhat as follows, the chief facts which we have learnt concerning the structure of the spinal cord, always keeping in view their physiological meaning.

The important feature of the spinal cord is the presence of what we have called 'grey matter,' and all our knowledge goes to shew that the important powers of the spinal cord, by which it differs from a thick multiple nerve, and by virtue of which we speak of it as a nervous centre or series of centres, are in some way or other associated with this grey matter.

With this grey matter the fibres of the spinal nerves are connected. The greater part of the fibres of the anterior root certainly end in or rather take origin from the grey matter close to the attachment of the root, and the rest most probably join the grey matter at no great distance. The fibres of the posterior root run, as we have seen, for some little distance in the white matter, but, if we except the special bundle which runs in the median posterior tract right up the cord to the bulb without joining the spinal grey matter at all, we may say that the fibres of the posterior root also join the grey matter not far from the attachment of the root.

Morphological reasons lead us, as we have seen, to regard the spinal cord as a series of segments, each segment corresponding to a pair of nerves; and even in the spinal cord of man we may recognize a segmental groundwork, obscured though this is by fusion and overlaid by the several commissural tracts. Each segment of this groundwork we may conceive of as a central mass of grey matter, connected on each side with an anterior and a posterior root, thus constituting a segmental nervous mechanism capable of carrying out certain functions.

Such a segment has been compared to a ganglion, but it differs strikingly from a ganglion, whether of the posterior root or of the splanchnic system, both in structure and in function. A ganglion and the grey matter of a spinal segment both contain nerve-cells, and so far resemble each other; but there the resemblance for the most part ends. In a ganglion the constituent nerve-cell is a development of the axis-cylinder of a fibre into a nucleated cell-body which lies on the course of the fibre, and may, as in a splanchnic ganglion, be placed just where one fibre divides into two or more. We have clear evidence that the cell, that is to say, the nucleus with the adjacent cell substance, exercises an important influence on the nutrition, and so on the functional activity of the nerve fibre; it acts as we have seen as a 'trophic centre.' There are also reasons for thinking that the cell-substance is more sensitive, more readily responsive to changes in its circumstances than is the axis-cylinder at some distance from the cell. But we have no satisfactory evidence that the cell can automatically originate nervous impulses in itself, as the outcome of its own intrinsic changes. Nor have we any evidence that the cell can exert any marked transforming power over the impulses passing along the fibre; the impulses which travel away from the cell do not appear to differ markedly from those which travel towards it.

The several instances in which there seemed to be evidence that splanchnic ganglia acted as centres either of reflex or of automatic action, have as we have seen broken down; and it is not even suggested that the ganglia of the posterior roots possess any such powers. The grey matter of the spinal cord, on the other hand, as we have already seen, and as we shall see more in detail, is especially characterized by the possession of reflex and automatic as well as of other powers.

In structure, moreover, such a spinal segment differs strikingly from a ganglion and exhibits features unknown in ganglia. In a ganglion the nerve fibres may divide, and in a small peripheral ganglion the division may give rise to very delicate fibrils; but the fibres or fibrils resulting from the division leave the ganglion to follow their appropriate courses; the division serves for dispersion only. In the spinal cord on the other hand both efferent and afferent fibres divide in such a way that their divisions are lost to view in the grey matter; division here seems to serve the purpose of union. The efferent fibre of the anterior root may be traced back as a process of a cell in the anterior horn. That cell gives off other processes, but no one of these processes is continued on as an axis-cylinder process stretching across the grey matter until it becomes a fibre of the posterior root, or as anything like such an axis-cylinder process. On the contrary, all the processes except the axis-cylinder process, divide into branches, and appear to end in nervous fibrils lost to view in the grey matter. Conversely, though our knowledge of the junction of the posterior fibres with the grey matter is much more imperfect than that of the junction of the anterior fibres, what we do know leads us to believe that the fibres of the posterior root, either by the mediation of cells, or by direct division of the axis-cylinder without the mediation of cells, similarly break up into fibrils and are similarly lost in the grey matter. All the evidence goes to shew that the anterior and posterior roots are functionally continuous; this functional continuity is, however, effected not by a gross continuity of axis-cylinders but in a peculiar manner through the division of branches of nerve cells or of axis-cylinders into the nervous tangle which forms such a special feature of the grey matter of the cord. We may perhaps venture to regard the grey matter of the segmental groundwork, of which we are now alone speaking, as constituting a nervous network or web, formed certainly in part by the rapidly dividing branches of nerve cells, and probably in part by the divisions of directly dividing nerve fibres.

In any ordinary section of the spinal cord the grey matter presents to view much more than this nervous groundwork. To say nothing of the indubitable neuroglia and the obscure structures, including small cells, which are claimed now to be neuroglia, now to be nervous in nature, the grey matter in every section shews numerous distinct nerve fibres crossing it in various directions; of these fibres a few are ordinary medullated fibres, some are non-medullated fibres, that is to say, are naked axis-cylinders, while others, and these the more numerous, are the peculiar medullated fibres of small diameter spoken of in § 563. A large number of these fibres, indeed all the larger ones, though they go to make up what we call grey matter, are not continuous with, and do not belong to the groundwork or nervous web, at all events, do not form part of the groundwork seen in the same section as themselves. They are simply fibres traversing the groundwork, in spaces of the neuroglia bed, on their way up or down the cord or across the cord from one part to another. It may be that some of the finer medullated fibres do really enter into the groundwork, and so contribute to the nervous web; but our knowledge is too imperfect to afford a clear decision on this point. Our inability to define its exact limits need not, however, prevent our recognizing the existence of the groundwork.

The prominence in this groundwork of the larger nerve-cells has led to the conception that the powers of the spinal segment are exercised by these nerve-cells to the exclusion of the other elements of the nervous web. But such a view has not been adequately proved. What we do know is that the nuclei and cell bodies of the cells of the anterior horn exercise an important influence on the nutrition of the fibres of the anterior root which proceed from them, and possibly also influence the nutrition of the other branches of the cells forming part of the groundwork; and these cells are probably so conspicuous a feature of every section of the spinal cord because of the important task entrusted to them of maintaining in due order the nutrition of the long stretch of motor fibres reaching from them to the muscular fibres or other peripheral organs. The fibres of the posterior root are not so obviously connected with the conspicuous cells of the grey matter; indeed as we have said it may be doubted, though the view is maintained by some, whether any cell intervenes to secure the continuity of a posterior fibre with the groundwork, a division of the axis-cylinder serving this purpose; and this becomes intelligible when we bear in mind that the posterior fibres are governed as far as their nutrition is concerned by the nerve cells of the ganglion on the posterior root, which ought probably to be considered as much a part of the spinal cord as the cells of the anterior horn. The nerve cell of the ganglion is adequate to secure the due nutrition of the nerve fibre until it joins the groundwork, and probably helps to maintain the nutrition of the groundwork itself.

Hence we may perhaps, until fresh evidence to the contrary is brought forward, incline to the view that the powers of the grey matter do not depend on the conspicuous cells alone or even chiefly, but on the peculiar molecular constitution and nature of the whole groundwork. The nuclei of the cells of the anterior horn with the cell substance adjacent to each and the cells of the ganglia on the posterior root probably govern the nutrition, and so the functional activity of the groundwork as well as of the issuing and entering fibres; but there appears to be as yet no convincing evidence of any other peculiar powers confined to the cells and absent from other parts of the groundwork. We may add that, in accordance with this view, the other cells of the grey matter, such as those of the vesicular cylinder, are to be regarded as of importance for governing the nutrition of fibres, commissural and others, starting from the spinal segment, and of the part of the groundwork from which by their mediation the fibres start, rather than for determining the functions of the groundwork of the segment or of the fibres receiving impulses from it.

§ **580**. The segmental groundwork of grey matter belonging to each pair of spinal nerves is so fused with that of all the other pairs, as to form along the whole length of the cord a mass of grey matter which appears, under certain circumstances at all events, to be continuous in the sense that impulses may pass in all directions along it. But each spinal segment is in addition connected by means of tracts of white matter with parts more or less distant. The crossed pyramidal tract is such a longitudinal commissural tract, connecting apparently each spinal segment in succession with a certain part of the cortex of the cerebrum. We have reason to think, as we shall see later on, that impulses descending this or that fibre or group of fibres of this tract give rise to the issue of motor impulses along this or that fibre or group of fibres of an anterior root. We do not at present know what is the exact manner by which the fibre in the pyramidal tract is connected with the fibre of the anterior root. It seems certain, however, that the connection is not in the form of a fibre isolated from the rest of the grey matter, continuing, so to speak, the pyramidal fibre into a cell of the anterior horn whence the fibre of the anterior root issues. Most probably the pyramidal fibre makes connections with the segmental groundwork spoken of above, whether with or without the intervention of a cell we cannot at present tell. The direct pyramidal tract is a like tract of less extent downwards, and the less known antero-lateral descending tract is probably of a similar nature.

The cerebellar and antero-lateral ascending tracts are in like manner to be regarded as longitudinal commissures between the successive spinal segments below and some part of the brain above. We have reason to think that these tracts convey upward impulses of a nature which may be called afferent, and are therefore in some way probably connected with the posterior roots. We do not know as yet the exact nature of the connection; but probably in those cases also, the commissural fibres are united not directly to the posterior fibres, but indirectly by means of the segmental groundwork. And since these tracts do not degenerate after section of the posterior roots, but only after section or other lesion of the cord itself, we may infer that their junction with the groundwork is effected by means of trophic cells, by means of some or other of the cells spoken of a little while before.

The median posterior tract seems to be a commissural tract of a nature different from any of the above. Through it a certain part of each posterior root is brought into connection, not with its own spinal segment but with the bulb above, and so with the brain, which thus receives direct representatives of each afferent spinal nerve. If however, as some maintain, the bundle in this tract starting from a spinal nerve below, diminishes as it proceeds upwards, throwing off fibres to pass elsewhere, though always carrying some fibres right up to the bulb, we must add to the above the further view that this tract connects also each posterior root, not with its own segment but with other more or less distant segments.

§ **581.** All the evidence which we possess goes to shew that each strand of each of these tracts runs isolated, that is to say, makes no connections with adjoining structures at any part of its course, from its beginning or end in the brain and its end or beginning in its appropriate spinal segment, or in the case of the median posterior tract from its beginning in the ganglion of a posterior root and its end in the bulb or in some distant spinal segment. In the crossed pyramidal tract, for instance, we have reason to think that one or more fibres run a quite unbroken and isolated course from the cortex of the cerebrum through various parts of the brain, along the whole length of the cord until they reach the lowermost spinal segmental mechanism. These tracts serve in no way to connect one segmental mechanism with another. The segmental mechanisms are however connected together; and the connections between them seem to be of two kinds. In the first place, as we have already suggested, the segmental pieces of grey matter are so fused together as to form what appears to be a continuity of grey matter from one end of the cord to the other. Though we cannot actually track our way histologically through, and are still less aware of the physiological nature of the labyrinth of nerve cells, fibres and fibrils which make up what we have called the groundwork, we may with considerable probability assume that the passage of nervous impulses along it is determined as much by the condition of the material as by its anatomical disposition; that, for instance, the restrictions to the flow of an impulse are brought about much more frequently by the refusal of the molecules of nervous matter to take up the molecular disturbance which is the essence of the impulse, that is to say, by molecular resistance, than by actual breaks of continuity in the nervous matter. Indeed we have some reasons for thinking that actual structural continuity of nervous material is not essential to functional continuity, that a nerve fibril for instance may produce its due effect on another nerve fibril or on a nerve cell, if sufficiently in contact with it, though the microscope fails to demonstrate actual continuity.

But besides the grey matter there are areas of white matter which do not belong either to the nerve roots as these are making their way into the grey matter, or to any of the tracts which we have mentioned. These comprise the strands of fibres which do not undergo either ascending or descending degeneration when parts of the spinal cord are injured or diseased. The area of white matter left when all the various tracts of ascending and descending degeneration detailed above are taken out, seems, at all events in the higher parts of the cord (Fig. 104) relatively small, and future observations may continue still further to reduce it; but it must be remembered, that none of the above mentioned tracts are 'pure'; they are all more or less mixed up, and some largely mixed up, with fibres which do not degenerate. Our knowledge is at present too scanty to allow us to make any statement with confidence concerning the function either of the fibres forming the white matter not yet marked out into tracts, or of the fibres scattered among the acknowledged tracts. But we may, at all events provisionally, assume that these fibres serve in the main as commissures connecting the successive segmental mechanisms with each other; we may conclude that changes taking place in one segmental mechanism can by means of these fibres produce correlated changes in some other distant segmental mechanism, without calling into action any of the grey matter of the intervening segmental mechanisms.

The commissures which we may suppose to be thus furnished by white matter are longitudinal commissures connecting the segmental mechanisms of the same lateral half of the spinal cord with each other. A transverse connection between the two lateral halves is afforded in some measure by the anterior white commissure. We shall see, however, later on reasons for thinking that many impulses besides those passing along the anterior commissure cross from one side of the cord to the other; and these whether they pass along distinct fibres or along the general groundwork must travel by the grey matter of the isthmus forming the anterior and posterior grey commissures.

Thus, as far as we can see at present, the spinal cord consists of a series of segmental mechanisms with their respective afferent and efferent roots, (the grey matter of the several segments being continuous along the cord) of encephalic ties of white matter between the several segments and the brain, of longitudinal commissural tracts connecting together the several segmental mechanisms, and of transverse commissures running largely in the grey matter.

SEC. 3. THE REFLEX ACTIONS OF THE SPINAL CORD.

§ 582. In the preceding portions of this work we have repeatedly seen that though we can learn much concerning the working of an organ, or tissue or part of the body by studying its behaviour when isolated from the rest of the body, all the conclusions thus gained have to be checked by a study of the behaviour of the same organ or part, while it is still an integral part of the intact body. All the several organs and tissues are so bound together by various ties, that the actions of each depend on the actions of the rest; and to say that the life of each part is a function of the life of the whole, is no less true than to say that the life of the whole is a function of the life of each part. This is especially borne in upon us, when we come to study the actions of the central nervous system. We may, on anatomical grounds, separate the spinal cord from the brain; but when we come to consider the respective functions of the two, we are brought face to face with the fact that in actual life a large part of the work of the brain is carried out by means of the spinal cord, and conversely the spinal cord does its work habitually under the influence of, if not at the direct bidding of the brain. We may gain certain conclusions by studying the behaviour of the spinal cord isolated from the brain, or of parts of the spinal cord isolated from each other; but we must be even more cautious than when we were dealing with other parts of the body, and must greatly hesitate to take it for granted that the work which we can make the spinal cord or a part of the spinal cord do, when isolated from the brain, is the work which is actually done in the intact body when the brain and spinal cord form an unbroken whole. Moreover this caution becomes increasingly necessary, when in our studies we pass from the simpler nervous system of one animal to the more complex nervous system of another; for it is by the complexity of their central nervous systems more than by any thing else, that the 'highest' animals are differentiated from those 'below' them.

When we compare a rabbit, a dog, a monkey and a man, the differences in the vascular, digestive and respiratory systems of the four, striking as they may appear, sink into insignificance compared with the differences exhibited by their respective central nervous systems. We need caution when from the results of experiments on dogs or rabbits, we draw conclusions as to the digestion or circulation of man, but we need far greater caution when from the behaviour of the isolated spinal cord of one of these animals we infer the behaviour of the intact spinal cord of man.

A further difficulty meets us when an experimental investigation entails operative interference with the central nervous system. Removal or section of, or other injury to parts of the brain or spinal cord is very apt to give rise in varying degree to what is known as 'shock'. The cutting or tearing or other lesion of any considerable mass of nervous substance affects the activity, not only of the structures immediately injured, but of other, it may be far distant, structures. The nature of 'shock' is not as yet thoroughly understood, but may perhaps, in part at all events, be explained by regarding the lesion as a very powerful stimulus, which, partly by way of inhibition but still more by way of exhaustion, depresses or suspends for a while normal functions, and thus gives rise to temporary diminution or loss of consciousness, of volition, of reflex movements and other nervous actions. Thus a section through the spinal cord, even when made with the sharpest instrument and with the utmost skill, so as to avoid all bruising as much as possible, may for a while suspend all reflex activity of the cord, or indeed all the obvious activities of the whole central nervous system. We may add that such a 'shock' of the central nervous system may also be produced by sudden lesions not bearing directly on the central nervous system, as for instance by extensive injury to a limb.

Moreover in many cases in which the effects of experimental interference have been watched for some considerable time, days, months or years after the operation, it has been observed, on the one hand, that phenomena which are conspicuous in the early period may eventually disappear, and, on the other hand, that activities which are at first absent may later on make their appearance; movements for instance which are at first frequent after a while die away, and conversely, movements which at first seemed impossible are later on easily achieved. We have to distinguish or to attempt to distinguish between the temporary and the lasting effects of the operation, including among the former not only those of ordinary 'shock,' but others of slower development or longer duration. In many instances where a part of the central nervous system is by section or otherwise suddenly separated from the rest, the phenomena suggest that the separated part is at first profoundly influenced as to its activities by the withdrawal of various influences which previously were being exerted upon it by the rest of the system, but later on accommodates itself to its new conditions, and learns, so to speak, to act without the help of those influences. And indeed it is possible that some of the effects of even immediate 'shock' may be due, not as suggested above, to the action of an inhibitory or exhausting stimulus, but to the sudden cessation of habitual influences.

Still, in spite of all these difficulties, it is possible not only to ascertain the working of an isolated portion of the central nervous system, but even to infer from the results some conclusions as to the share taken by that portion in the working of the entire and intact system. There can be no doubt, for instance, that the spinal cord can, quite apart from the brain, carry out various reflex actions, and that moreover it does carry out actions of this kind when in the intact organism it is working in concert with the brain. Indeed the carrying out of various reflex actions seems to be one of the most important functions of the spinal cord, so much so that, though the brain or, at least, parts of the brain can also and do develope reflex actions, the spinal cord offers the best field for the study of these actions. We have already (§ 101) touched on the general features of reflex actions, and elsewhere have incidentally dwelt on particular instances; we may therefore confine ourselves now to certain points of special interest.

§ **583**. Reflex movements are perhaps best studied in the frog and other cold-blooded animals, since in these the actions of the cord are less dependent on, and hence less obscured by the working of, the other parts of the central nervous system. They obtain however in the warm-blooded mammal also, but in these special precautions are necessary to secure their full development. In the frog the shock, which as we have said follows upon division of the spinal cord and for a while suspends reflex activity, soon passes away; within a very short time after the bulb for instance has been divided the most complicated reflex movements can be carried on by the frog's spinal cord when the appropriate stimuli are applied. With the mammal the case is very different. For days even after division of the spinal cord the parts of the body supplied by nerves springing from the cord below the section may exhibit very feeble reactions only. In the dog, for instance, after division of the spinal cord in the lower dorsal region, the hind limbs hang flaccid and motionless, and pinching the hind foot evokes as a response either slight irregular movements or none at all. Indeed were our observations limited to this period we might infer that the reflex actions of the spinal cord in the mammal were but feeble and insignificant. If however the animal be kept alive for a longer period, for weeks or better still for months, though no union or regeneration of the spinal cord takes place, reflex movements of a powerful, varied and complex character manifest themselves in the hind limbs and hinder parts of the body; a very feeble stimulus applied to the skin of these regions promptly gives rise to extensive and yet coordinate movements. Indeed the more the matter is studied, the stronger is the evidence that the reflex movements carried out by isolated portions of the spinal cord of the mammal are hardly less definite, complete and purposeful, than those witnessed in the frog. It is worthy of attention, as bearing out the remarks made above on the great differentiation of the central nervous system in the higher animals, that the reflex phenomena in mammals vary very much not only in different species but also in different individuals and in the same individual under different circumstances. Race, age, and previous training, seem to have a marked effect in determining the extent and character of the reflex actions which the spinal cord is capable of carrying out; and these seem also to be largely influenced by passing circumstances, such as whether food has been recently taken or no. It has been asserted that the isolated spinal cord of the rabbit, which has been the subject of so many experiments, is, as compared with that of the dog and many other mammals, singularly deficient in the power of carrying out complex reflex movements.

In studying reflex actions in man we are met with the difficulty that we never have to deal with a portion of the spinal cord separated from the rest of the central nervous system under the favourable circumstances of experimental investigation. In man, we must be content to examine reflex actions either while the whole nervous system is intact, or when a portion of the cord has been wholly or partially separated by some more or less diffuse disease or by some accident involving more or less crushing of the nervous structures. Hence, the caution already given, as to drawing inferences concerning man from the results of experiments on animals, acquires still greater force.

§ **584.** Confining ourselves at first to the results of experiments on animals we may say that in both cold-blooded and warm-blooded animals the salient feature of ordinary reflex actions is their purposeful character, though every variety of movement may be witnessed, from a simple spasm to a most complex manœuvre. And in all reflex movements, both simple and complex, we can recognize certain determining influences which more or less directly contribute to the shaping of this purposeful character.

Thus the features of any movement taking place as part of a reflex action are in part determined by the characters of the afferent impulses. Simple nervous impulses generated by the direct stimulation of afferent nerve fibres generally evoke as reflex movements merely irregular spasms in a few muscles; whereas the more complicated differentiated sensory impulses generated by the application of the stimulus to the skin, readily give rise to large and purposeful movements. It is easier to produce a complex reflex action by a slight pressure on or other stimulation of the skin than by even strong induction-shocks applied directly to a nerve trunk. If, in a brainless frog, the area of skin supplied by one of the dorsal cutaneous nerves be separated by section from the rest of the skin of the back, the nerve being left attached to the piece of skin and carefully protected from injury, it will be found that slight stimuli applied to the surface of the piece of skin easily evoke reflex actions, whereas the trunk of the nerve may be stimulated with even strong currents without producing anything more than irregular movements. In ordinary mechanical and chemical stimulation of the skin it is not a single impulse but a series of impulses which passes upwards along the sensory nerve, the changes in which may be compared to the changes in a motor nerve during tetanus. In every reflex action, in fact, the central mechanism may be looked upon as being thrown into activity through a summation of the afferent impulses reaching it. Hence while a reflex action is readily called forth by even feeble induction-shocks applied to the skin if they be repeated sufficiently rapidly, a solitary induction-shock is ineffectual unless it be strong enough to cause in the skin or nerves changes of an electrolytic nature sufficient to give rise of themselves to a series of impulses.

§ **585**. When a muscle is thrown into contraction in a reflex action, the pitch of the sound which it gives forth does not vary with the stimulus, but is constant, being the same as that given forth by a muscle thrown into contraction by the will. From which we infer, even bearing in mind the discussion in § 80 concerning the nature of the muscular sound, that in a reflex action the afferent impulses do not simply pass through the centre in the same way that they pass along afferent nerves, but are profoundly modified. And in accordance with this we find, as we shall see, that a reflex action takes up an amount of time, the greater part of which is spent in the carrying out of the central changes, and which though variable is always much longer, and may be very much longer, than that taken up by the mere passage of a nervous impulse along a corresponding length of nerve fibre. The term reflex action is therefore an unsuitable one. The afferent impulse is not simply reflected or turned aside into an efferent channel; on its arrival at the centre it starts changes of a different nature from and more complex than its own; and the issue of efferent impulse is the result of those more complex changes not the mere continuation of the simpler afferent impulse. In other words, the interval between the advent at the central organ of afferent, and the exit from it of efferent impulses, is a busy time for the nervous substance of that organ; during it many processes, of which we have at present very little exact knowledge, are being carried on.

§ **586**. The character of the movement forming part of a reflex action is also influenced by the intensity of the stimulus. A slight stimulus, such as gentle contact of the skin with some body, will produce one kind of movement; and a strong stimulus, such as a sharp prick applied to the same spot of skin, will call forth quite a different movement. When a decapitated snake or newt is suspended and the skin of the tail lightly touched with the finger, the tail bends towards the finger; when the skin is pricked or burnt, the tail is turned away from the offending object. And so in many other instances. It must be remembered of course that a difference in the intensity of the stimulus entails a difference in the characters of the afferent impulses; gentle contact gives rise to what we call a sensation of touch, while a sharp prick gives rise to pain, consciousness being differently affected in the two cases because the afferent impulses are different. Hence the instances in question are in reality fuller illustrations of the dependence, to which we called attention above, of the characters of a reflex movement on the characters of the afferent impulses.

Further, as we have already pointed out (§ 101) while the motor impulses started by a weak stimulus applied to an afferent nerve are transmitted along a few, those started by a strong stimulus may spread to many efferent nerves. Granting that any particular afferent nerve is more especially associated with certain efferent nerves than with any others, so that the reflex impulses generated by afferent impulses entering the cord by the former pass with the least resistance down the latter, we must evidently admit further that other efferent nerves are also, though less directly, connected with the same afferent nerve, the passage into the second efferent nerve meeting with a greater but not an insuperable resistance. When a frog is poisoned with strychnia, a slight touch on any part of the skin may cause convulsions of the whole body; that is to say, the afferent impulses passing along any single afferent nerve may give rise to the discharge of efferent impulses along any or all of the efferent nerves. This proves that a physiological if not an anatomical continuity obtains between all the parts of the spinal cord which are concerned in reflex action, that the nervous network intervening between the afferent and efferent fibres forms along the whole length of the cord a functionally continuous field. This continuous network however we must suppose to be marked out into tracts presenting greater or less resistance to the progress of the impulses into which afferent impulses, coming along this or that afferent nerve, are transformed on their advent at the network; and accordingly the path of any series of impulses in the network will be determined largely by the energy of the afferent impulses. And the action of strychnia may be in part explained by supposing that it reduces and equalises the normal resistance of this network, so that even weak impulses travel over all its tracts with great ease.

§ 587. Further, the movement, forming part of a reflex action, varies in character according to the particular part of the body to which the stimulus is applied. The reflex actions developed by stimulation of the internal viscera are different from those excited by stimulation of the skin. We have reason to think that the contraction of or other changes in a skeletal muscle may produce, by reflex action, contractions of other muscles; and such reflex actions also differ from those started by stimulation of the skin. In reflex actions started by applying a stimulus to the skin the movements vary largely according to the particular area of the skin which is affected. Thus, pinching the folds of skin surrounding the anus of the frog produces different effects from those witnessed when the flank or toe is pinched; and, speaking generally, the stimulation of a particular spot calls forth particular movements. In the case of the simpler reflex movements, it appears to be a general rule that a movement started by the stimulation of a sensory surface or region on one side of the body, is developed on the same side of the body, and if it spreads to the other side, still remains most intense on the same side; the movement on the other side moreover is symmetrical with that on the same side. It has been maintained that 'crossed' or diagonal reflex movements, as where stimulation of one fore-foot leads to movements of the opposite hind-limb, do not occur unless some portion of the bulb be left attached to the spinal cord. Seeing that locomotion in four-footed animals is largely effected by diagonal movements of the limbs, one would rather have expected to find the spinal cord itself provided with mechanisms to assist in carrying them out; and indeed it is affirmed that in the case of cold-blooded animals and of many young mammals, after division of the spinal cord below the bulb, a gentle stimulation will provoke a diagonal movement, slight pressure on one fore-foot for example giving rise to movements in the opposite hind-leg; a strong stimulus however will produce an ordinary one-sided movement. Again, when in a dog the cord has been divided in the lower thoracic region so that the hind limbs depend on the lumbar cord alone, a rhythmically repeated drawing up and letting down of the hind limbs is witnessed when these are allowed to hang down; and these movements, which appear to be of a reflex nature excited by the pendant position of the limbs, are often seen to alternate regularly in the two limbs, the right leg being extended while the left leg is being drawn up and vice versa. It may further be observed that if the foot of one pendant limb be pinched while the other limb is passively flexed the flexion of the limb which is pinched is accompanied by an extension of the other limb. In these respects however different animals, as already urged, differ from each other.

§ **588**. From these and similar phenomena we may infer that the nervous network spoken of above is, so to speak, mapped out into nervous mechanisms by the establishment of lines of greater or less resistance, so that the disturbances in it generated by certain afferent impulses are directed into certain efferent channels. It may be added that though conspicuously purposeful movements seem to need the concurrent action of several segments of the cord, and as a rule, the greater the length of the cord involved the more complex and the more distinctly purposeful the movement, still the movements evoked by even a segment of the cord may be purposeful in character; hence we must conclude that every segment of the nervous network is mapped out into mechanisms. But the arrangement of these mechanisms, especially of the more complex ones, is not a fixed and rigid one. We cannot always predict exactly the nature of the movement which will result from the stimulation of any particular spot, because the result will vary according to the condition of the spinal cord, especially in relation to the strength and character of the stimulus. Moreover, under a change of circumstances a movement quite different from the normal one may make its appearance. Thus when a drop of acid is placed on the right flank of a brainless frog, the right foot is almost invariably used to rub off the acid; in this there appears nothing more than a mere 'mechanical' reflex action. If however the right leg be cut off, or the right foot be otherwise hindered from rubbing off the acid, the left foot is, under the exceptional circumstances, used for the purpose. This at first sight looks like an intelligent choice. A choice it evidently is; and were there many instances of choice, and were there any evidence of a variable automatism, like that which we call 'volition', being manifested by the spinal cord of the frog, we should be justified in supposing that the choice was determined by an intelligence. But, as we shall have occasion later on to point out, a frog, deprived of its brain so that the spinal cord only is left, makes no spontaneous movements at all. Such an entire absence of spontaneity is wholly inconsistent with the possession of intelligence. Then again the above experiment, if not the only instance, is at all events by far the most striking instance of choice on the part of a brainless frog. We are therefore led to conclude that the phenomena must be explained in some other way than by being referred to the working of an intelligence. Moreover this conclusion is supported by the behaviour of other animals. Thus similar vicarious reflex movements may be witnessed in mammals, though not perhaps to such a striking extent as in frogs. In dogs, in which partial removal of the cerebral hemispheres has apparently heightened the reflex excitability of the spinal cord, the remarkable scratching movements of the hind leg which are called forth by stimulating a particular spot on the loins or side of the body, are executed by the leg of the opposite side, if the leg of the same side be gently held. In this case the vicarious movements are ineffectual, the leg not being, as in the case of the frog, crossed over so as to bear on the spot stimulated, and can not be considered as betokening intelligence. Again the 'mechanical' nature of reflex actions is well illustrated by the behaviour of a decapitated snake. When the body of the animal in this condition is brought into contact at several places at once with an arm or a stick, complex reflex movements are excited, the obvious purpose as well as effect of which is to twine the body round the object. A decapitated snake will however with equal and fatal readiness twine itself round a red-hot bar of iron, which is made to touch its skin in several places at the same time.

§ 589. In considering the nature of the events in the spinal cord which determine the behaviour of the frog in the instance just mentioned we must bear in mind that the movements in question are 'coordinated;' that is to say not only are many distinct muscles brought into play but certain relations are maintained between the amount, duration and exact time of occurrence of the contraction of each muscle and those of the contractions of its fellow muscles sharing in the movement. In the absence of such coordination the movement would become irregular and ineffectual. We shall have occasion later on in dealing with voluntary movements to point out that the coordination and hence the due accomplishment of a voluntary movement is dependent on certain afferent impulses passing up from the contracting muscles to the central nervous system, and guiding the discharge of the efferent impulses which call forth the contractions. When these afferent impulses affect consciousness we speak of them as constituting a 'muscular sense;' it is, as we shall see, by the 'muscular sense' that we become aware of and can appreciate the condition of our muscles. But we have reason to think that the afferent impulses which constitute the basis of the muscular sense, whatever be their exact nature, in order to play their part in bringing about the coordination of a voluntary movement need not pass right up to the brain and develope a distinct muscular 'sense,' but may produce their effect by working on the nervous mechanisms of the spinal cord with which the motor fibres carrying out the movement are connected. In other words, the coordination of a voluntary movement takes place in the part of the spinal cord which carries out the movement, and not in the brain, though the latter may be conscious of the whole movement including its coordination.

But if the spinal cord possesses mechanisms for carrying out coordinated movements, which in the case of voluntary movements are discharged by nervous impulses descending from the brain, we may infer that in reflex actions the same mechanisms are brought into action though they are discharged by afferent impulses coming along afferent nerves instead of by impulses descending from the brain. The movements of reflex origin, in all their features except their exciting cause, appear identical with voluntary movements; the two can only be distinguished from each other by a knowledge of the exciting cause. And it seems unreasonable to suppose that the spinal cord should possess two sets of mechanisms in all respects identical save that the one is discharged by volitional impulses from the brain and the other by afferent impulses from afferent nerves.

We are led therefore to the conclusion that in a reflex action two kinds of afferent impulses are concerned: the ordinary afferent impulses which discharge the nervous mechanism within the cord and so provoke the movement, and the afferent impulses which connect that nervous mechanism with the muscles about to be called into play, and which take part in the coordination of the movement provoked. The nature of these latter afferent impulses is at present obscure; we know as yet little more than the fact of their existence; but if we admit, as we seem compelled to do, that the character of a reflex action is determined by them as well as by the afferent impulses which actually discharge the mechanism, it seems possible that a fuller knowledge of these coordinating afferent impulses may afford an adequate explanation of the fact that when, as in the case of the frog in question, the usual set of muscles cannot be employed by the nervous mechanism, recourse is had to another set.

We have avoided the introduction of the word 'consciousness' as unnecessarily complicating the question; and it would be out of place to discuss psychological problems here. We may remark however that since we have no objective proofs of consciousness outside ourselves, and only infer by analogy that such and such an act is an outcome of consciousness on account of its likeness to acts which are the outcome of our own consciousness, we conclude that the brainless frog possesses no active consciousness like our own, because absence of spontaneous movements seems to be irreconcilable with the existence of an active consciousness whose very essence is a series of changes. Consciousness as we recognize it seems to be necessarily operating as, or to be indissolubly associated with the presence of, an incessantly repeated internal stimulus; and we cannot conceive of that stimulus failing to excite mechanisms of movement which, as in the case of the brainless frog, are confessedly present. We may however distinguish between an active continuous consciousness, such as we usually understand by the term, and a passing or momentary condition, which we may speak of as consciousness, but which is wholly discontinuous from an antecedent or from a subsequent similar momentary condition; and indeed we may suppose that the complete consciousness of ourselves, and the similarly complete consciousness which we infer to exist in many animals, has been gradually evolved out of such a rudimentary consciousness. We may, on this view, suppose that every nervous action of a certain intensity or character is accompanied by some amount of consciousness, which we may, in a way, compare to the light emitted when a combustion previously giving rise to invisible heat waxes fiercer. We may thus infer that when the brainless frog is stirred by some stimulus to a reflex act, the spinal cord is lit up by a momentary flash of consciousness coming out of darkness and dying away into darkness again; and we may perhaps further infer that such a passing consciousness is the better developed the larger the portion of the cord involved in the reflex act and the more complex the movement. But such a momentary flash, even if we admit its existence, is something very different from consciousness as ordinarily understood, is far removed from intelligence, and cannot be appealed to as explaining the 'choice' spoken of above.

§ **590**. Lastly, the characters of a reflex movement are, as we need hardly say, dependent on the intrinsic condition of the cord. The action of strychnia just alluded to is an instance of an apparent augmentation of reflex action best explained by supposing that the resistances in the cord are lessened. There are probably however cases in which the explosive energy of the nervous substance is positively increased above the normal. Conversely, by various influences of a depressing character, as by various anæsthetics or other poisons, reflex action may be lessened or prevented; and this again may arise either from an increase of resistance, or from a diminution in the actual discharge of energy. So also, various diseases may so affect the spinal cord as to produce on the one hand increased reflex excitability so that a mere touch may produce a violent movement, and on the other hand diminished reflex excitability so that it becomes difficult or impossible to call forth a reflex action.

§ **591**. When we come to study the reflex actions of man we should at first perhaps be inclined to infer that, since in him the spinal cord is so largely used as the instrument of the brain, the independent reflex actions of the cord, at least such as affect skeletal muscles, are in him of much less importance than they appear to be in animals; and experience seems to support this view. But it must be remembered that in his case, as we have already stated (§ 583), we lack the guidance of experimental results; we are obliged to trust to the entangled phenomena of disease or to a study of the behaviour of the cord while it is still a part of an intact nervous system; and each of these methods presents difficulties of its own. The movements, which in the intact human body we can recognize as indubitable reflex actions, are as a rule simple and unimportant. They are, in by far the greater number of instances, occasioned by stimulation of the skin or of the mucous membrane, for the most part involve a few muscles only, and rarely indicate any very complex coordination. The flexion, followed by extension, of the leg which is called forth by tickling the sole of the foot, or the winking of the eye when the cornea or conjunctiva is touched, may perhaps be regarded as the type of these movements. A very common form of reflex action is that in which a muscle or group of muscles is thrown into contraction by stimulation of the overlying or neighbouring skin, as when the abdominal muscles contract upon stroking the skin of the abdomen or the testicle is retracted upon stroking the inside of the thigh. A reflex movement may occur as the result of stimulation of an organ of special sense, parts of the central nervous system other than the spinal cord serving as the centre. A sound or a flash of light readily produces a start, a bright light makes the eye wink and may cause a person to sneeze (the greater coordination manifest in this act being due to the fact that the complex respiratory mechanism is brought into play, § 391), and reflex movements may result from a taste or smell. A special form of reflex action, or at least an action resembling a reflex action, is called forth by sharply striking certain tendons; for instance striking the tendon below the patella gives rise to a sudden extension of the leg, known as the "knee-jerk"; but it will be best to discuss these 'tendon reflexes' or 'muscle reflexes' as they are called later on in another connection.

On the whole the reflex movements carried out by the intact nervous system of man are we repeat scanty and comparatively simple; but we are not justified in inferring from this that the human spinal cord, left to itself, is incapable of doing more, that owing to the predominant activity of the brain it has lost the powers possessed by the spinal cord in the lower animals. For it may be that the cord, when joined to the brain, is through various influences proceeding from the latter in a different condition from that in which it is when separated from the brain; indeed we have reason to think that this is so; and we may here remark that in the lower animals, as in man, the development of reflex movements is difficult and uncertain in the presence of the brain.

When we turn to the teaching of disease however, we again find that reflex movements carried out by the cord or by parts of the cord are, on the whole, scanty and simple.

In some stages of certain diseases of the spinal cord extensive reflex movements are witnessed; but these are not purposeful coordinated movements, such as have been described above as occurring in frogs and mammals after experimental interference, but rather mere exaggerations of the simpler reflex movements witnessed when the nervous system is intact. In cases of paraplegia (such being the term generally used when disease or injury has cut off the cord, generally the lower part of the cord, from the brain so that the will cannot bring about movements in, and the mind derives no sensations from, the parts below the lesion, the legs for instance), it sometimes happens that contact with the bedclothes, or other external objects, sets up from time to time rhythmically repeated movements, the legs being alternately drawn up and thrust out again. And an exaggeration of the 'knee-jerk' or other 'tendon reflexes' is a very common symptom in certain spinal diseases. It is rarely if ever that reflex movements of a really complicated character are observed. Moreover clinical experience shews that in man, when a portion of the cord is isolated, reflex actions carried out by means of that portion so far from being exaggerated are much more commonly exceeding feeble or absent altogether. In the cases in which the physiological continuity of the lower with the upper part of the cord has been broken by disease, by some growth invading the nervous structures or by some changes of the nervous structures themselves, we may attempt to explain the absence from the lower part of coordinate reflex activity, such as is seen in the lower animals, as due to the disease not only affecting the powers of the actually diseased part, but influencing the whole cord below, and either by inhibition, of which we shall speak presently, or in some other way depressing its functions. But the same absence of complex reflex movements is also often observed in cases in which the cord has been severed by accident, and indeed, though accidental injuries to the human cord generally produce more profound and extensive mischief than that which results in animals from skilful experimental interference, clinical experience tends, on the whole, to support the view that in man the more complete subordination of the spinal cord to the brain has led to the dying out of the complex reflex actions which are so conspicuous in the lower animals. This however cannot be regarded as distinctly proved.

When we come to study voluntary movements we shall see reason to think that in man, as in the lower animals, the will in carrying out these movements makes use of complex nervous mechanisms situated in the spinal cord, nervous mechanisms into the working of which, as urged above, afferent impulses enter largely; and it seems improbable that these spinal mechanisms should be capable of being thrown into action by the will only. In the act of walking for instance it is highly probable that the movements of the legs are the direct results of the action of nervous mechanisms in the lumbar cord brought into play by the will, being thus, in an indirect manner only, the products of volitional impulses; and even in man, though clinical experience only affords us instances of this machinery working apart from the brain in a damaged condition and under unfavourable circumstances so that the resemblance of the movements observed to the complete act of walking is but feeble, still it seems similarly probable that under more favourable circumstances the lumbar cord separated from the brain might as part of a reflex act carry out the movements in a more complete and coordinate manner.

§ 592. We have dwelt above chiefly on reflex actions, in which the efferent impulses cause contractions of skeletal muscles since these are undoubtedly the most common and the most prominent forms of reflex action; but it must not be forgotten that the efferent impulses of reflex origin may produce contractions of other muscles, as well as other effects, such as secretion for instance. On several of these we have dwelt, from time to time in previous parts of this work, and it will be unnecessary to repeat them here. But it may be worth while to point out that the spinal cord by serving as a reflex centre for innumerable ties which correlate the nutritive or metabolic activities of the several tissues to events taking place in other parts of the body, plays a conspicuous part in securing the welfare of the whole body. In dealing (§ 549) with the general problems of nutrition, we stated that an orderly nutrition appears to be in some way dependent on nervous influences. Many of these nervous influences appear to issue from the spinal cord, either as parts of a reflex act, or as the outcome of some automatic processes. When in a dog the lumbar cord is wholly separated from the rest of the cord by section, the nutrition of the hind limbs, and the general health of the animal may, with care, be maintained in a very satisfactory condition; but if that small separated piece of the cord be destroyed death inevitably ensues before long, in spite of every care and precaution, being brought about apparently by the disordered nutrition of the hind limbs and other parts supplied by nerves coming from the lumbar cord. In man, extensive injuries to the spinal cord are followed by bed sores and other results of impaired nutrition; and indeed death is generally brought about in this way, in cases of paraplegia caused by accidental crushing or severance of the cord. The scarcity of well marked reflex actions mentioned above as characteristic of such cases, may perhaps be due to the fact that these disorders of nutrition prevent the patient living long enough for the separated cord to recover the functions which properly belong to it.

§ **593.** *Inhibition of Reflex Action.* The reflex actions of the spinal cord, like other nervous actions, may be totally or partially inhibited, that is to say may be arrested or hindered in their developement by impulses reaching the centre while it is already in action. Thus if the body of a decapitated snake be allowed to hang down, slow rhythmic pendulous movements, which appear to be reflex in nature, soon make their appearance, and these may be for a while arrested by slight stimulation, as by gently stroking the tail. We have already seen that the action of such nervous centres as the respiratory and vaso-motor centres, which frequently at all events is of a reflex nature, may be either inhibited or augmented by afferent impulses. The micturition centre in the mammal, which is also largely a reflex centre, may be easily inhibited by impulses passing downward to the lumbar cord from the brain, or upward along the sciatic nerves. In the case of dogs, whose spinal cord has been divided in the thoracic region, micturition set up as a reflex act by simple pressure on the abdomen or by sponging the anus, is at once stopped by sharply pinching the skin of the leg. And it is a matter of common experience that in man micturition may be suddenly checked by an emotion or other cerebral event. The erection centre in the lumbar cord, also in large measure a reflex centre, is similarly susceptible of being inhibited by impulses reaching it from various sources. And indeed many similar instances of the inhibition of reflex movements might readily be quoted.

Several apparent instances of the inhibition of reflex acts are not really such: in these cases all the nervous processes of the act may take place in their entirety and yet fail to produce their effect on account of a failure in the muscular part of the act. Thus when we ourselves by an effort of the will stop the reflex movements which otherwise would be produced by tickling the soles of the feet, we achieve this to a large extent by throwing voluntarily into action certain muscles, the contractions of which antagonise the action of the muscles engaged in carrying out the reflex movements. But it may be doubted even in these cases, whether inhibition is always or wholly to be explained in this way; and certainly in very many instances of reflex inhibition, no such muscular antagonism is present, and the reflex act is checked at its nervous centre.

When the brain of a frog is removed, and the effects of shock have passed away, reflex actions are developed much more readily and to a much greater degree than in the entire animal, and in mammals also reflex excitability has been observed to be increased by removal of the cerebral hemispheres. This suggests the idea that in the intact nervous system the brain is habitually exerting some influence on the spinal cord tending to prevent the normal development of the spinal reflex actions. And we learn by experiment that stimulation of certain parts of the brain has a remarkable effect on reflex action. If a frog, from which the cerebral hemispheres have been removed (the optic lobes, bulb and spinal cord being left intact), be suspended by the jaw, and the toes of the pendent legs be from time to time dipped into very dilute sulphuric acid, a certain average time will be found to elapse between the dipping of the toe and the resulting withdrawal of the foot. If, however, the optic lobes or optic thalami be stimulated, as by putting a crystal of sodium chloride on them, it will be found on repeating the experiment while these structures are still under the influence of the stimulation, that the time intervening between the action of the acid on the toe and the withdrawal of the foot is very much prolonged. That is to say, the stimulation of the optic lobes has caused impulses to descend to the cord, which have there so interfered with the nervous processes engaged in carrying out reflex actions as greatly to retard the generation of efferent impulses, or in other words, has inhibited the reflex action of the cord. And similar results may be obtained in mammals by stimulating certain parts of the corpora quadrigemina, which bodies are homologous to the optic lobes of frogs. From this it has been inferred that there is present in this part of the brain a special mechanism for inhibiting the reflex actions of the spinal cord, the impulses descending from this mechanism to the various centres of reflex action being of a specific inhibitory nature. But, as we have already seen, impulses of an ordinary kind, passing along ordinary sensory nerves, may inhibit reflex action. We have quoted instances where a slight stimulus, as in the pendulous movements of the snake, and where a stronger stimulus as in the case of the micturition of the dog, may produce an inhibitory result; we may add that in the frog adequately strong stimuli applied to any afferent nerve will inhibit, *i.e.* will retard or even wholly prevent reflex action. If the toes of one leg are dipped into dilute sulphuric acid at a time when the sciatic of the other leg is being powerfully stimulated with an interrupted current the period of incubation of the reflex act will be found to be much prolonged, and in some cases the reflex withdrawal of the foot will not take place at all. And this holds good, not only in the complete absence of the optic lobes and bulb, but also when only a portion of the spinal cord, sufficient to carry out the reflex action in the usual way, is left. There can be no question here of any specific inhibitory centres, such as have been supposed to exist in the optic lobes. But if it is clear that inhibition of reflex action may be brought about by impulses which are not in themselves of a specific inhibitory nature, we may hesitate to accept the view that a special inhibitory mechanism in the sense of one giving rise to nothing but inhibitory impulses is present in the optic lobes of frogs, and after removal of the brain that the exaltation of reflex actions which is manifest is due to the withdrawal of such a specific inhibitory mechanism.

The presence of the brain does obviously produce an effect which may be broadly spoken of as inhibitory, and a specific action of the brain, in an effort of the will, may stop or inhibit a specific reflex action; but we must not in these matters be led too much away by the analogy of the special and limited cardiac inhibitory mechanism. There we have apparently to deal with fibres, whose exclusive duty it is to convey inhibitory impulses from the bulb to the cardiac muscle, and inhibition of the heart, at least through nervous influences, is exclusively carried out by them. But already, in studying the nervous mechanism of respiration, we have seen reason to think that afferent impulses passing along the same nerves and probably along the same fibres may, according to circumstances, now inhibit, now augment the respiratory centre, and have thus been led to speak of inhibitory impulses, that is impulses producing an inhibitory effect, apart from specific inhibitory fibres. In the complex working of the central nervous system, we may still more expect to come across similar instances of the same channels serving as the path, either of inhibition or of augmentation. In all probability, actions or processes, which we may speak of as inhibitory, do play, as indeed we shall see, an important part in the whole work of the central nervous system; in all probability many of the phenomena of nervous life are the outcome of a contest between what we may call inhibitory and exciting or augmenting forces; but in all probability also we ought rather to seek for the explanation of how vagus impulses inhibit the beat of the heart by reference to the inhibitory phenomena of the central nervous system, than to attempt to explain the latter by the little we know of the former. At present, however, we must be content with the fact that experiments on animals shew that the brain, not only by some action or other may inhibit particular spinal reflex movements, but also habitually exercises a restraining influence on the reflex activity of the whole cord, though we are unable to state clearly how this inhibition is carried out.

We say 'experiments on animals' because though we know, as stated above, by an appeal to our own consciousness, that an action of the brain, an effort of the will, may stop a particular reflex act, we have no evidence that in man separation of the cord from the brain leads, as in animals, to heightened reflex activity. In diseases, or injuries to the cord, reflex actions are, as we have said, sometimes exaggerated, but it is possible and indeed probable that the increase is due to the morbid processes producing a greater irritability of the cord itself, and not to the withdrawal of any inhibitory influences. In many cases, in perhaps the greater number, no exaggeration but a diminution or even absence of reflex activity is observed; so much so that could we trust explicitly to clinical experience, we should be inclined to conclude that the scantiness of spinal reflex action in man was due not to any preoccupation of the cord by influences proceeding from a dominant brain, but to an inherent paucity of spinal reflex mechanisms. But we have already said all we have at present to say on this point.

§ **594**. *The Time required for Reflex Actions.* When one eyelid is stimulated with a sharp electrical shock, both eyelids blink. Hence, if the length of time intervening between the stimulation of the right eyelid and the movement of the left eyelid be measured, this will give the total time required for the various processes which make up a reflex action. It has been found to be from ·0662 to ·0578 sec. Deducting from these figures the time required for the passage of afferent and efferent impulses along the fifth and facial nerves to and from the bulb, and for the latent period of the contraction of the orbicularis muscle, there would remain ·0555 to ·0471 sec. for the time consumed in the central operations of the reflex act. The calculations, however, necessary for this reduction, it need not be said, are open to sources of error; moreover the reflex act in question is carried out by the bulb and not by the spinal cord proper. Blinking thus produced is a reflex act of the very simplest kind; but as we have seen in the preceding pages, reflex acts differ very widely in nature and character; and we accordingly find, as indeed we have incidentally mentioned, that the time taken up by a reflex movement varies very largely. This indeed is seen in blinking itself. When the blinking is caused not by an electric shock applied to the eyelid, but by a flash of light falling on the retina, in which case complex visual processes are involved, the time is distinctly prolonged; moreover the results in different experiments in which light serves as the stimulus are not nearly so uniform as when the blinking is caused by stimulation of the eyelid.

In general it may be said that the time required for any reflex act varies very considerably with the strength of the stimulus employed, being less for the stronger stimuli; this we should expect, seeing that the efferent impulses of the reflex act are not simply afferent impulses transmitted through the central organ, but result from internal changes in the central organ started by the afferent impulse or impulses; and these internal changes will naturally be more intense and more rapidly effected when the afferent impulses are strong. It is stated that when the movement induced is on the same side of the body as the surface stimulation of which starts the act, the time taken up is less than when the movement is on the other side of the body, allowance being made for the length of central nervous matter involved in the two cases; that is to say the central operations of a reflex act are propagated more rapidly along the cord than across the cord. The rapidity of the act varies of course with the condition of the spinal cord, the act being greatly prolonged when the cord becomes exhausted; and a similar delay has been observed in cases of disease. The time thus occupied by purely reflex actions must not be confounded with the interval required when the changes taking place in the central nervous system are of a more complicated nature, and more or less distinctly involve mental operations; of the latter we shall speak later on.

SEC. 4. THE AUTOMATIC ACTIONS OF THE SPINAL CORD.

§ 595. We speak of an action of an organ or of a living body as being spontaneous or automatic when it appears to be not immediately due to any changes in the circumstances in which the organ or body is placed, but to be the result of changes arising in the organ or body itself and determined by causes other than the influences of the circumstances of the moment. Some automatic actions are of a continued character; others, like the beat of the heart, are repeated in regular rhythm; but the most striking automatic actions of the living body, those which we attribute to the working of the will and which we call voluntary or volitional, are characterized by their apparent irregularity and variableness. Such variable automatic actions form the most striking features of an intact nervous system, but are conspicuously absent from a spinal cord when the brain has been removed.

A brainless frog placed in a condition of complete equilibrium in which no stimulus is brought to bear on it, protected for instance from sudden passing changes in temperature, from a too rapid evaporation by the skin and the like, remains perfectly motionless until it dies. Such apparently spontaneous movements as are occasionally witnessed are so few and seldom, that we can hardly do otherwise than attribute them to some stimulus, internal or external, which has escaped observation. In the mammal (dog) after division of the spinal cord in the dorsal region regular and apparently spontaneous movements may be observed in the parts governed by the lumbar cord. When the animal has thoroughly recovered from the operation the hind limbs rarely remain quiet for any long period; they move restlessly in various ways; and when the animal is suspended by the upper part of the body, the pendent hind limbs are continually being drawn up and let down again with a monotonous rhythmic regularity, suggestive of automatic rhythmic discharges from the central mechanisms of the cord. In the newly born mammal too, after removal of the brain, movements apparently spontaneous in nature are frequently observed. But all these movements, even when most highly developed, are very different from the movements, irregular and variable in their occurrence though orderly and purposeful in their character, which we recognize as distinctly voluntary. Even admitting that some of the movements of the brainless mammal may resemble voluntary movements in so far as they are due to changes taking place in the spinal cord itself independent of the immediate influence of any stimulus, we are not thereby justified in speaking of the spinal cord as developing a will in the sense that we attribute a will to the brain.

§ **596**. In the case of the beat of the heart, the automatic rhythmic discharge of energy appears to be exclusively the outcome of the molecular nutritive changes taking place in the cardiac substance. The beat may be modified, as we have seen, by nervous impulses reaching the cardiac substance along certain nerves; but the actual existence of the beat is wholly independent of these extraneous influences; the rhythmic discharge continues when they are entirely absent. The automatic rhythmic discharge of respiratory impulses from the respiratory centre is also dependent on the intrinsic molecular changes of the centre, these being, as we have seen, largely determined by the character of the blood streaming through it; but in this case extrinsic nervous impulses, reaching the centre along the vagus and other nerves, play a much more important part than do similar impulses in the case of the heart. They act so continually on the centre and enter so largely into its working, that we are compelled to regard the activity of the centre as fed, if we may use the word, not only by the intrinsic molecular nutritive processes of the centre itself, but also by the extrinsic nervous influences which flow into the centre from without. The automatism of the spinal cord as a whole resembles, in this aspect, that of the respiratory centre rather than that of the heart. It has for its basis doubtless the intrinsic molecular changes of the grey matter, on whose remarkable constitution we dwelt in a previous section; the metabolic events of this substance are so ordered as to give rise to discharges of energy; but the discharge appears to be also intimately dependent on the inflow into the grey matter of afferent impulses and influences. The normal discharge of efferent impulses from the cord undoubtedly takes place under the influence of these incoming impulses; and it may be doubted whether the grey matter of the cord would be able, in the absence of all afferent impulses, to generate any sustained series of discharges out of its merely nutritive intrinsic changes. The automatic activity of the cord is fed not only by intrinsic nutritive events, but also by extrinsic influences.

In this feature we may, moreover, find perhaps the reason why the automatic activity of the spinal cord is so limited, as compared with that of the brain. In spite of certain striking but superficial characters of which we shall speak later on, the grey matter of the brain presents no histological features so different from those of the grey matter of the cord, as to justify us in concluding that the one is capable and the other incapable of developing the impulses, which we call volitional, out of the molecular nutritive changes of its substance. We are, therefore, led to the conclusion that the fuller automatic activity of the brain is due to the intrinsic changes of its substance being so much more largely assisted by the influx of various afferent impulses and influences, notably those of the special senses. To this question, however, we shall have to return later on.

§ **597.** In treating of the vascular system we saw that the central nervous system exercised through the vaso-motor nerves such an influence on the muscular coats of the blood vessels as to maintain, what we spoke of as 'tone,' section of vaso-constrictor fibres leading to "loss of tone." We saw further, that arterial tone, though normally dependent on the general vaso-motor centre in the bulb, could be kept up by the cord itself, that for instance a tone of the blood vessels of the hind-limbs could be maintained by the isolated dorso-lumbar cord. This maintenance of arterial tone may be spoken of as one of the "automatic" functions of the spinal cord. We have also seen that plain muscular fibres, other than those of the arteries, notably the fibres forming sphincters, such as the cardiac and pyloric sphincters of the stomach, the sphincter of the bladder, and especially the sphincter of the anus, also possess tone, and that the tone of these sphincters is also dependent on the spinal cord, or on some part of the central nervous system. We need not repeat the discussions concerning these mechanisms and other instances of the spinal cord exercising an automatic influence over various viscera; we have referred to them here, since they serve as an introduction to a question which has been much debated, and which has many collateral and important bearings, namely the question whether the spinal cord exercises an automatic function in maintaining a tone of the skeletal muscles.

The question is not one which, like the case of arterial tone, can be settled off hand by a simple experiment. Most observers agree that the section of a motor nerve does not produce any clearly recognizable immediate lengthening of a muscle supplied by the nerve, in the same way that section of a vaso-constrictor nerve undoubtedly gives rise to a relaxation of the muscular fibres in the arteries governed by it; and it has been inferred from this that skeletal tone does not exist. But there are several facts to be taken into consideration before we can come to a just decision.

The skeletal muscles have been described as being placed "on the stretch" in the living body. If a muscle be cut away from its attachments at each end, it shortens; if it be cut across, it gapes.

In other words, the muscle in the living body possesses a latent tendency to shorten, which is continually being counteracted by its disposition and attachments. In studying muscular contraction we saw (§ 87) that the shortening of a contraction is followed by a relaxation or return to the former length, both the contraction and relaxation being the result of molecular changes in the living muscular substance. We have now to extend our view and to recognize that, apart from the occurrence of ordinary contractions, molecular changes are by means of nutritive processes continually going on in the muscle in such a way that the muscle, though continually on the stretch, does not permanently lengthen, but retains the power to shorten upon removal or lessening of the stretch, and conversely though possessing this power of shortening permits itself to lengthen when the stretch is increased. In this way the muscle is able to accommodate itself to variations in the amount of stretch to which it is from time to time subjected. When a flexor muscle for instance contracts, the antagonistic extensor muscle is put on an increased stretch and is correspondingly lengthened; when the contraction of the flexor passes off the extensor returns to its previous length; and so in other instances. Thus by virtue of certain changes within itself a muscle maintains what may be called its natural length in the body, always returning to that natural length both after being shortened and after being stretched. In this the muscle does no more than do the other tissues of the body which, within limits, retain their natural form under the varied stress and strain of life; but the property is conspicuous in the muscle; and its effects in skeletal muscles correspond so closely to those of arterial tone, that we may venture to speak of it as skeletal tone. Indeed, the molecular changes at the bottom of both are probably the same.

These changes are an expression of the life of the muscle; they disappear when the muscle dies and enters into rigor mortis; and moreover, during life they vary in intensity so that the 'tone' varies in amount according to the nutritive changes going on. We have seen reason to believe that the nutrition of a muscle as of other tissues is governed in some way by the central nervous system. We saw, in treating of muscle and nerve (§ 83), that the irritability of a muscle is markedly affected by the section of its nerve, *i.e.* by severance from the central nervous system; and again (§ 549) in speaking of the so-called trophic action of the nervous system, we referred to changes in the nutrition of muscles occasioned by diseases of the nervous system. And experience, especially clinical experience, shews that the nutritive changes which determine tone are very closely dependent on a due action of the central nervous system. When we handle the limb of a healthy man, we find that it offers a certain amount of resistance to passive movements. This resistance, which is quite independent of, that is to say, which may be clearly recognized in the absence of all distinct muscular contractions of volitional or other origin, is an expression of muscular tone, of the effort of the various muscles to maintain their 'natural' length. In many cases of disease this resistance is felt to be obviously less than normal; the limb is spoken of as "limp" or "flabby;" or as having 'a want of tone.' In other cases of disease, on the other hand, this resistance is markedly increased; the limb is felt to be stiff or rigid; more or less force is needed to change it from a flexed to an extended, or from an extended to a flexed condition; and, in the range of disease, we may meet with very varying amounts of increased resistance, from a condition which is only slightly above the normal to one of extreme rigidity. In some cases the condition of the muscle is such as at first sight seems much more comparable to a permanent ordinary contraction than to a mere exaggeration of normal tone; but all intermediate stages are met with; and indeed these extreme cases may be taken as indicating that the molecular processes which maintain what we are now calling tone, are at bottom, of the same nature as those which carry out a contraction; they serve to shew the fundamental identity of the skeletal tone with the more obvious arterial tone.

Clinical experience then shews that the central nervous system does exert on the skeletal muscles such an influence as to give rise to what we may speak of as skeletal tone, changes in the central nervous system, leading in some cases to diminution or loss of tone, in other cases to exaggeration of tone, manifested often as conspicuous rigidity. The question why the changes take one direction in one case and another in another is one of great difficulty (the occurrence of extreme rigidity being especially obscure), and cannot be discussed here. We have called attention to the facts simply because they shew the existence of skeletal tone and its dependence on the central nervous system. This conclusion is confirmed by experiments on animals, and these also afford proof that in animals the spinal cord can by itself, apart from the brain, maintain the existence of such a tone. In a frog, after division of the cord below the brain, the limbs during the period of shock are flabby and toneless; but after a while, as the shock passes off, tone returns to the muscles, and the limbs offer when handled a resistance like that of the limbs of an entire frog. When the animal is suspended the hind limbs do not hang perfectly limp and helpless, but assume a definite position; and that this position is due to some influence proceeding from the spinal cord is shewn by dividing the sciatic nerve on one side; the hind limb on that side now hangs quite helpless. This more pendent position shews that some of the flexors have lengthened in consequence of the section of the nerve, and this result may be taken as refuting the argument, quoted above against the existence of tone, which is based on the statement that a muscle cannot be observed to lengthen after section of its nerve. It may be here remarked that if the brainless frog, whose hind-limbs are more or less pendent when the body is suspended, be placed on its belly the hind-limbs are brought into a flexed position under the body by means of obvious muscular contraction; and from this it might be inferred that the maintenance of the position of the pendent limb was also the result of a feeble contraction. But no obvious contractions can be observed in the latter case, as in the former; and when in the former the limb has once been brought into the flexed position, that position, like the pendent position, is maintained without obvious contractions. As we said above 'tone' may pass into something which appears to be identical with a contraction, but where no obvious contractions are observed it seems preferable to speak of the state of the muscle as one of tone.

In the dog, after division of the cord in the thoracic region, the hind-limbs during the period of shock are limp and toneless. In the warm blooded animal, as we have said, the effects of shock are much more lasting than in the cold blooded animal; and in the dog the tone of the skeletal muscle returns much more slowly than in the frog. Indeed when the division of the cord has taken place low down the skeletal tone returns very slowly, and may be manifested very feebly, or even be absent altogether. But under favourable circumstances, when a sufficient length of cord has been left, a fairly normal tone is reestablished. In man, in accordance with the facts previously mentioned (§ 591) skeletal tone, which has been lost through the continuity of the cord being broken by disease or accident, appears rarely if ever to return fully in the regions below the lesion.

We may therefore on the whole of the evidence conclude that the maintenance of skeletal tone is one of the functions of the cord; but we may here repeat that the condition of the cord, on which depends the issue from the cord along efferent nerves of the influences, whatever their nature, which produce tone in the muscle, may be, and indeed is, in its turn dependent on afferent impulses. In the case of the frog quoted above the tone of the pendent limbs disappears or is greatly lessened when the posterior roots of the sciatic nerves are divided, though the anterior roots be left intact. In the absence of the usual stream of afferent impulses passing into it, the cord ceases to send forth the influences which maintain the tone. Hence the maintenance of tone presents many analogies with a reflex action especially when we remember that, as stated above, tone passes insensibly into contraction; and it may seem a mere matter of words whether we speak of the maintenance of tone as an automatic or as a reflex action of the cord. We may, however, distinguish the part played by the afferent impulses in assisting the cord to a condition in which it is capable of maintaining tone from the part played by an afferent impulse in causing a reflex action; in the former the action of the afferent impulses seems analogous to that of a supply of arterial blood in maintaining an adequate irritability of the nervous substance, in the latter the afferent impulses lead directly to a discharge of energy. And it is convenient to distinguish the two things by different names.

§ **598**. The close connection between tone and reflex action is illustrated by the so-called 'tendon-phenomena,' which, on the one hand, are considered as cases of ordinary reflex action, and, on the other hand, have been regarded as exemplifying a special influence of the spinal cord on the irritability of the muscles. It is well known that when the leg is placed in an easy position, resting for instance on the other leg, a sharp blow on the patellar tendon will cause a sudden jerk forward of the leg, brought about by a contraction of the quadriceps femoris; it is necessary or at least desirable for a good development of the jerk that the tendon (and muscle) should be somewhat on the stretch. Similarly the muscles of the calf may be thrown into action by tapping the tendo Achillis put somewhat on the stretch by flexion of the foot; and in some cases the same muscles may be made to execute a series of regular rhythmic contractions, called 'clonic' contractions, by suddenly pressing back the sole of the foot so as to put them on the stretch. These, and other instances of a like kind, at first sight appear to be, and indeed are by many observers maintained to be, cases of reflex action, due to afferent impulses started in the tendon; hence they have been frequently spoken of as 'tendon-reflex.' Other observers maintain that they are not reflex, but due to direct stimulation of the muscles, the vibrations set up in the more or less tense tendon being transmitted to the muscles and so throwing the latter into contractions. The chief arguments against their being reflex are that the interval between the tap and the contraction is very short ·03 or ·04 sec., shorter than the ordinary interval of a reflex action (§ 594) and that the movement persists after section of the nerves of the tendon. The first argument is perhaps not a very strong one, and the second may be met by supposing that, in such a case at least, if not always, the reflex act really begins in the muscle being started in it by the vibrations transmitted to it along the tendon.

But even if we admit that the movements are purely muscular, started and carried out in the muscle without the help of the usual reflex chain of afferent impulses, spinal centre and efferent impulses, we must at the same time admit that they are closely dependent on the integrity of the spinal cord and of the connections between the cord and the muscle. In the case of animals they disappear when the spinal cord is destroyed, or the nerves going to the muscles are severed, or even when the posterior roots only are divided. The measure of their development both in animals and in man is also closely dependent on the condition of the spinal cord and of the central nervous system generally. They may be increased or diminished, augmented or inhibited by a coincident voluntary effort directed towards some other end, or by the coincident development of a sufficiently distinct sensation. In general it may be said that whatever favours the activity of the spinal cord tends to increase them, and whatever depresses the activity of the spinal cord tends to diminish them. They are diminished or wanting in certain diseases of the spinal cord (*e.g.* locomotor ataxy), and exaggerated in others; so much so indeed that they have become of practical clinical importance as a means of diagnosis. Whether we regard them as instances of ordinary reflex action, or consider that they are carried out by the muscle itself and that the cord intervenes only so far as to increase, maintain or diminish the irritability of the muscular substance, it remains good that they are prominent whenever the conditions increase the reflex or other excitability of the cord, and diminish or disappear when the conditions lower or abolish that excitability.

§ **599**. Disease in man reveals other actions of the spinal cord which bear features different from those of an ordinary reflex movement, and yet have been described as reflex in nature. For instance certain affections of the cord are characterized by the legs becoming rigid in extreme extension, the rigidity of the straightened limbs being often so great, that when a bystander lifts up one leg from the bed, the other leg is raised at the same time. The rigidity is due to the extensor muscles being thrown into a state of contraction, which is so uniform and long continued that it may be spoken of as a "tonic" contraction; such a tonic rigidity may however be replaced by a series of rhythmic, "clonic," contractions. It has sometimes been observed that the limbs when flexed are supple and free from rigidity, but that rigidity sets in so soon as they are brought into the position of extension, the leg becoming suddenly fixed and straight somewhat in the way that a clasp-knife springs back when opened. It seems clear that the peculiar contraction is carried out by means of the spinal cord, but the whole action, though it is often spoken of as a 'muscle-reflex,' is very unlike an ordinary reflex movement. In an ordinary movement an extensor is brought into action when a limb is flexed, not when it is already extended; and if in a reflex act the condition of the muscle about to be thrown into action determines in any way the discharge of impulses from the reflex centre, we should expect that the stretching of an extensor muscle by flexion, not its relaxation by extension, would determine the discharge of extensor impulses. In the case of the diseases in question just the opposite seems to take place; the position which appears to determine the development of the remarkable contraction is precisely that in which the strain upon the extensors is at its minimum. It may be doubted, therefore, whether the word reflex should be used to denote such phenomena; but the phenomena themselves deserve attention, especially perhaps as shewing how in the disorders of the grey matter of the cord due to disease impulses or influences which are latent only in health become actual and effective.

It remains for us to speak of the part played by the spinal cord, as the instrument of the brain, in the execution of voluntary movements and in the development of conscious sensations; but it will be best to consider these matters in connection with the brain itself, to the study of which we must now turn.

CHAPTER II.

THE BRAIN.

SEC. 1. ON SOME GENERAL FEATURES OF THE STRUCTURE OF THE BRAIN.

§ 600. It would be out of place to attempt to give here a complete description of the structure of the brain; but certain features must be kept fresh in the mind as a basis for physiological discussion; and to these we must now turn our attention, a general acquaintance with the topographical anatomy of the brain being presupposed[1].

Like the spinal cord the brain consists of 'white matter,' in which the nervous elements are almost exclusively medullated fibres, and of 'grey matter,' in which nerve-cells and other nervous elements are also present; but the grey matter of the brain is much more variable in structure than that of the spinal cord, and possesses features peculiar to itself; these we shall study later on.

For physiological purposes the brain may be conveniently divided into parts corresponding to the divisions which appear in it in the embryo. At an early stage in the life of the embryo, that part of the medullary tube which is about to become the brain differs from that which is about to become the spinal cord, in that the central canal, which in the latter is of fairly uniform bore along its whole length, is in the former alternately widened and narrowed, so that the tube forms a series of vesicles, the cerebral vesicles, succeeding each other lengthways. At first these vesicles are three in number, called respectively fore-brain, mid-brain, and hind-brain; but the fore-brain after having developed on each side a lateral vesicle, the optic vesicle, subsequently transformed into the retina and optic nerve, gives rise in front of itself to a pair of vesicles placed side by side, or rather to a single vesicle with a deep median furrow, the vesicle of the cerebrum, containing a cavity divided by a median partition into two cavities, lying side by side, which open into the cavity of the original fore-brain by a Y-shaped opening. This embryonic chain of vesicles is developed into the adult brain by unequal growth of the walls and unequal expansion of the cavities, certain features being also impressed upon it by the bend on the longitudinal axis, which takes place in the region of the mid-brain and is known as the cranial flexure.

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[1] Figs. 108 to 123 which will be found in succeeding sections may with advantage be consulted in reading this section though not specially referred to in the text.

§ **601**. In the hind part of the hinder vesicle or hind-brain, the ventral, basal portion or floor is thickened to form the *bulb*, while the greater part of the dorsal portion or roof does not thicken at all, is not transformed into nervous elements, but remains as a single layer of epithelium, adherent to the pia mater overlying it, and so forms a thin covering to the lozenge-shaped cavity of the vesicle, now known as the *fourth ventricle*.

In the front part of the same hind-brain, on the contrary, the roof and sides are enormously developed into the conspicuous *cerebellum* overhanging the front part of the fourth ventricle, while the floor is also thickened into the *pons Varolii*.

This thickening of the pons is largely made up on the one hand of horizontal nerve fibres, which run transversely from each side of the cerebellum into the pons or from one side of the cerebellum to the other, and on the other hand of longitudinal fibres, which run forwards from the bulb and are wrapped round by and interlaced with the others. At the front margin of the pons these longitudinal fibres, augmented in number, appear as two thick strands, the *crura cerebri*, forming the floor of the mid-brain, the roof of which is thickened into the *corpora quadrigemina*, and the cavity of which is reduced to a narrow tubular passage, the *aqueduct of Sylvius*, or *iter a tertio ad quartum ventriculum*.

At the level of the fore-brain the crura cerebri, diverging rapidly from each other as they pass forwards, leave the median portion of the floor of the vesicle now known as the *third ventricle* very thin, but form, especially behind and ventrally, thick lateral walls, which are further increased in thickness by the development on each side of a mass largely composed of grey matter, known as the *optic thalamus*. The roof of the third ventricle, like that of the fourth ventricle, is not developed into nervous elements but remains extremely thin, and consists of nothing more than a single layer of epithelium.

§ **602**. In front of the third ventricle each diverging crus cerebri spreads out in a radial fashion into the corresponding half of the paired vesicle of the cerebrum now developed into the preponderant *cerebral hemispheres*, the two cavities of which are now known as the *lateral ventricles.* The growth of the cerebral hemispheres is not only much greater than that of the rest of the brain, but also takes place in a special manner. At their first appearance the cerebral hemispheres lie wholly in front of the fore-brain or vesicle of the third ventricle, but in their subsequent growth while expanding in nearly all directions they extend especially backwards. Thus in the adult brain, on the dorsal surface they not only completely cover up the third ventricle but also overlap the mid-brain, reaching so far back as to cover the front border of the cerebellum, while on the ventral surface, though in the middle line they leave exposed the floor or ventral portions of the walls of the third ventricle, at the sides they are seen to reach as far backward as on the dorsal surface. The median furrow on the dorsal surface which separates each hemisphere from its fellow is at first shallow but rapidly deepens, so that as the hemispheres grow they become separated from each other by a narrow deep longitudinal fissure, into which as we shall see a fold of the dura mater dips. This fissure is not only deep vertically, i.e. from the dorsal surface ventrally, but at the front of the brain runs backward in the middle line almost as far as the level of the third ventricle, so as completely to separate from each other the anterior parts of each hemisphere, known as the anterior lobes; at the back of the brain also it similarly runs forward in the middle line for a considerable distance, so as to separate from each other the posterior lobes. Hence the two great masses of the cerebral hemisphere are united with each other, not along their whole length but for about a third of that length, the isthmus or bridge thus connecting them lying at some depth below the dorsal surface at the bottom of the longitudinal fissure, in about the middle third of its length.

At its first appearance each lateral ventricle is of a more or less oval form, its walls are of uniform thickness, and it lies in front of the third ventricle. During the growth of the hemispheres it acquires a peculiar shape and becomes divided into an anterior cornu or horn stretching into the anterior portion, a posterior horn stretching into the posterior portion, and a descending horn, which curves laterally and ventrally into the middle portion of the hemisphere; owing to the great backward extension of the hemispheres the lateral ventricles come to lie not only in front of but also at the side of, and indeed, to a certain extent, above or dorsal to the third ventricle; and during the growth of the parts the originally wide Y-shaped opening which placed the hind ends of the two lateral ventricles in communication with the front of the third ventricle becomes narrowed into a slit-like passage of similar form, the foramen of Monro, which still opening into the front of the third ventricle, now leads on each side from a point rather in front of the middle of the lateral ventricle.

As the hemisphere enlarges the growth of the walls of the vesicle is not uniform in all parts. At an early period there may be observed in the ventral wall or floor of the vesicle a thickening, which assuming a special, more or less semilunar, form and projecting into the cavity becomes the body known as the *corpus striatum.* As development proceeds the corpus striatum on each side becomes attached to the optic thalamus, lying behind and to the median side of itself, the radiating fibres of the crus cerebri passing between the two, and also as we shall see dividing the corpus striatum into two bodies, called the *nucleus caudatus* and *nucleus lenticularis.* A notable result of this growth and change of position of the hemispheres and of the coalescence of the corpus striatum with the optic thalamus is that the latter body, though really belonging to the third ventricle, comes to project somewhat into the lateral ventricle; a strip of the upper surface of the optic thalamus, along its outer, lateral edge, forms a portion of the floor of the lateral ventricle in the median region on each side of the third ventricle. Besides this special development of the corpus striatum, the walls of each vesicle, with the exception of the median part by which the two vesicles coalesce with each other, become (we are now speaking of the higher mammals) thickened much in the same way all over, the surface being folded so as to give rise to convolutions or *gyri* separated by furrows or *sulci;* and the thickening taking place in such a way as to give the ventricle its peculiar shape. The median coalesced part undergoes a different and peculiar change. This part, which at first lies in front of the third ventricle, through the changes brought about by the growth of the hemispheres so shifts its position as to lie immediately over, dorsal to the third ventricle, very much as if this part of the cerebral vesicles had been folded back over the fore-brain. In the junction itself we may distinguish a dorsal and a ventral portion. The dorsal portion is developed into a system of transverse commissural fibres passing across from one hemisphere to the other. In the median region these fibres form a thick compact band, called the *corpus callosum,* which may be exposed to view at the bottom of the longitudinal fissure, while on each side they spread away in all directions to nearly all parts of the surface of the hemispheres, passing over and helping to form the roof of the lateral ventricles. The band is not flat but curved ventralwards; hence in a longitudinal vertical section of the brain taken in the middle line it presents a curved form with the concavity directed ventralwards. While this dorsal portion of the junction is developed at the sides as well as in the middle line, the ventral portion is developed in the median region only, and that in a special way, so that it forms below, ventral to, the corpus callosum an arched plate, in the shape of a triangle with the apex directed forwards, called the *fornix,* which lies immediately above the thin epithelial roof of the third ventricle. In front, the narrower apical portion of the fornix lies at some little distance below, ventral to, the corpus callosum, and here the junction between the two vesicles is reduced to a thin sheet, the *septum lucidum;* but behind, the broader basal portion of the fornix is arched up so as to lie immediately under and touch the corpus callosum. Hence the septum lucidum has the form of a more or less triangular vertical sheet, broad in front and narrowing behind, separating the two lateral ventricles. The sheet may be conceived of as being double and formed by the apposition of two layers, one belonging to each ventricle; between these two layers is developed a narrow closed cavity containing fluid, called the *fifth ventricle.* But while the lateral ventricles open by the foramen of Monro into the third ventricle and the third ventricle is continuous by means of the aqueduct with the fourth ventricle, which again passes into the central canal of the spinal cord, the whole series being developed out of the same embryonic neural canal, the fifth ventricle communicates with none of them; it is a cavity of different origin.

The corpus callosum or dorsal portion of the junction between the vesicles spreads out, as we have said, laterally along its whole length, and thus forms a broad band joining the two hemispheres together; the middle portion spreads out in a more or less straight direction though curving over the ventricle upwards and downwards to reach various parts of the hemisphere, while the front and hind ends bend round on each side forwards and backwards to reach the anterior and posterior parts. Thus through the corpus callosum the thick wall of one ventricle is made continuous with that of the other. The disposition of the fornix or ventral portion of the junction is very different. At its apex in front the fornix bifurcates into two bands, known as the pillars of the fornix, which on each side become continuous with, and take a peculiar course in the walls of the third ventricle. In like manner behind, the angles of the base of the fornix are continuous with the walls of the lateral ventricles, that is to say, with the thick mass of the hemispheres, being also prolonged as two special strands of fibres called the crura of the fornix. But along each side of the triangle, between the attachments in front and behind, the substance of the fornix is not continued into the substance of the corresponding hemisphere; the edge of the fornix appears on each side to lie loose on the dorsal surface of the optic thalamus, which here forms the median portion of the floor of the lateral ventricle; between the optic thalamus below and the fornix above there seems to be a narrow slit by which the cavity of the lateral ventricle communicates with parts outside itself. In reality however there is no actual breach of continuity though there is a breach of nervous substance. The slit is bridged over by a layer of epithelium, by means of which the edge of the fornix is made continuous with the upper surface of the optic thalamus, and the median wall of the lateral ventricle made complete. But this layer of epithelium has the following peculiar relations to the pia mater covering the brain.

We have said that the roof of the third ventricle, like that of the fourth ventricle, consists only of a layer of epithelium devoid of nervous elements. We have further seen that the fornix, and the hind part of the corpus callosum with which it is continuous overlie the third ventricle, the free base of the fornix with the rounded hind end of the corpus callosum above forming together the hind border of the junction or bridge between the two hemispheres. The pia mater covering the dorsal surface of the brain, passing forwards under this curved border, spreads over the top of the third ventricle, becoming adherent to the layer of epithelium just referred to, and thus forms a vascular sheet called the *velum interpositum*, which serves as the actual roof of the third ventricle, immediately below, ventral to, the fornix; it cannot be seen without previously removing the fornix. At the lateral edge of the fornix, on each side, this same vascular sheet of pia mater projects from beneath the fornix into the lateral ventricle carrying with it the layer of epithelium which, as we said, made the edge of the fornix actually continuous with the rest of the walls of the lateral ventricle; the part of the pia mater thus seen projecting beyond the edge of the fornix when the lateral ventricle is laid open is called the *choroid plexus*. To this peculiar intrusion of the pia mater, by which the nutrition of the brain is assisted, we shall return when we come to speak of the vascular arrangements of the brain. Meanwhile we may point out, that while this vascular ingrowth seems to make the cavity of the third ventricle continuous with that of the lateral ventricle on each side, and all three with the exterior of the brain, it really does not do so. The cavity of the third ventricle is made complete by the layer of epithelium forming its roof, and the cavity of the lateral ventricle is made complete by the layer of epithelium passing from the lateral edge of the fornix over the choroid plexus to the other parts of the wall of the ventricle. To pass along this line from the actual cavity of the lateral into that of the third ventricle one must first pierce the epithelium covering the choroid plexus, thus gaining access to the pia mater of the plexus and of the velum, and then again pierce the epithelium coating the under surface of the velum and forming the roof of the third ventricle. It is only by the foramen of Monro that a real communication exists between the cavity of the lateral and that of the third ventricle.

Thus by the large growth and backward extension of the cerebral hemispheres, the third ventricle comes to form as it were the front end of the cerebrospinal axis, the crura cerebri expanding on each side of the third ventricle into the cerebral hemispheres which cover up the ventricle on the dorsal surface but leave its walls exposed on the ventral surface. Attached to the dorsal surface of the third ventricle at its hind end, ventral to and somewhat projecting beyond the base of the fornix, lies the pineal gland with its attachments, the remnants of a once-important median organ; and attached to the ventral surface of the ventricle, at the apex of a funnel-shaped projection, the infundibulum, lies the pituitary body, also a remnant of important ancestral structures.

§ 603. We may then divide the whole brain into a series of parts corresponding to the main divisions of the embryonic brain. At the front lie the cerebral hemispheres, with the lateral ventricles, developed out of the cerebral vesicles; and with these are associated the corpora striata, the term cerebral hemisphere being sometimes used so as to include these bodies, and sometimes so as to exclude them. Next come, corresponding to the original fore-brain, the parts forming the walls of the third ventricle, conspicuous among which are the optic thalami; for these bodies though they appear to intrude into the lateral ventricles belong properly to the third ventricle. In the mid-brain which follows, the cavity, now the tubular passage of the aqueduct, is roofed in by the two pairs, anterior and posterior, of corpora quadrigemina, the dimensions of which are not very great; but a thick floor is furnished by the crura cerebri. In each crus we must distinguish between a dorsal portion called the *tegmentum*, in which a large quantity of grey matter is present and in which a great complexity in the arrangement of fibres exists, and a ventral portion, the *pes* or *crusta*, which is a much more uniform mass of longitudinally disposed fibres. As the crura passing forward diverge into the cerebral hemisphere on each side, the tegmentum ceases at the hinder end and ventral parts of the optic thalamus; it is the pes which supplies the mass of fibres radiating into each cerebral hemisphere. In a view of the ventral surface of the brain, the base of the brain as it is frequently called, the crura may be seen emerging from the anterior border of the pons. This we have spoken of as the thickened floor of the front part of the hind-brain, but in reality, it encroaches a little on the mid-brain, the hind part of the corpora quadrigemina being in the same dorsoventral plane as the front part of the pons (see Fig. 108). In the main, however, the pons belongs to the fore part of the hind-brain, the roof and sides of which are developed as we have said into the cerebellum. This superficially resembles the cerebral hemispheres in its large size, and in the special development of its surface, which is formed of grey matter folded in a remarkable manner and often spoken of as cortex. The cerebellum, though the lateral portions, called the hemispheres, project above the median portion, called the vermis, is, unlike the cerebrum, a single mass; each lateral half however sends down ventrally a mass of fibres which, running transversely, partly end in the pons and partly are continued across the pons into the other lateral half; this mass of fibres, thus constituting as we have said a considerable part of the pons, forms on each side, just as it leaves the cerebellum to enter the pons, a thick strand, called the *middle peduncle* of the cerebellum. From the cerebellum there also proceeds backwards into the bulb on each side a thick strand of fibres, the *inferior peduncle* of the cerebellum or restiform body; and a third strand, the *superior peduncle* of the cerebellum, passes forwards on each side into the region of the corpora quadrigemina. As the latter converge towards each other behind the corpora quadrigemina the angle between them is filled up by a thin sheet of nervous matter, the *valve of Vieussens*, which thus for a little distance backwards forms a roof for the front part of the fourth ventricle, just where the lozenge-shaped cavity is narrowing to become the aqueduct. Behind the cerebellum and pons comes the bulb, which as we have said is the thickened floor of the hind part of the hind-brain, the roof of the cavity being here practically wanting.

Of these several divisions, the first division, that of the cerebral hemispheres, including the corpora striata, stands apart from the rest by reason both of its origin and the character of its development. As we shall see, this anatomical distinction corresponds to a physiological difference.

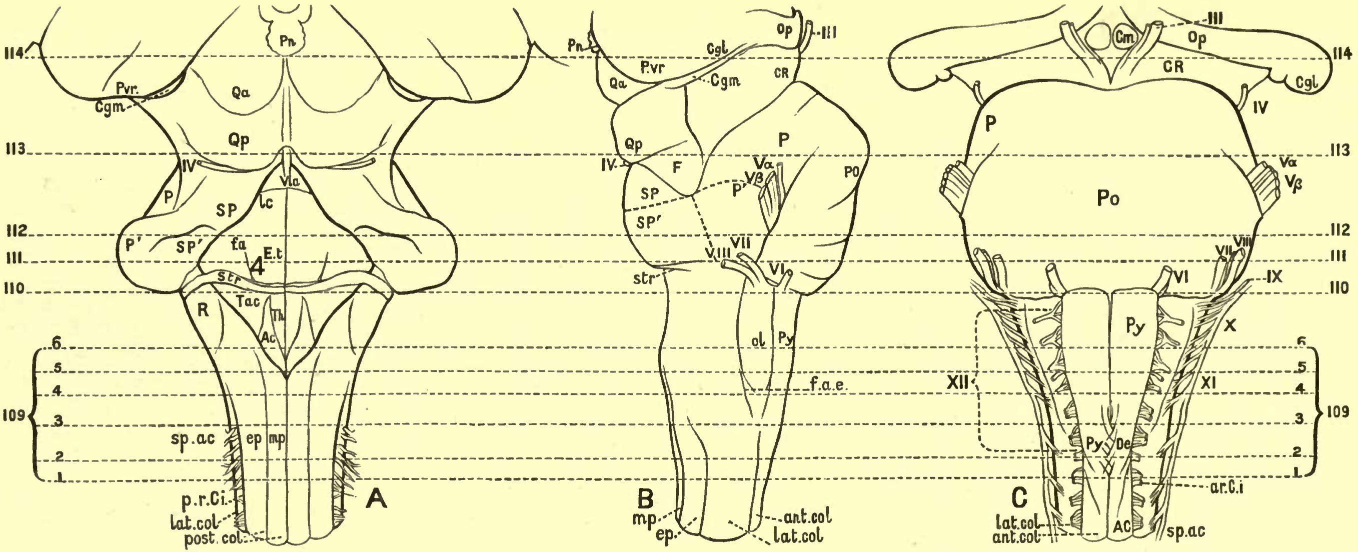
Of the other parts of the brain the crura cerebri deserve special attention. We may regard these as starting in the cord but largely augmented in the bulb; they traverse the pons, where they are still further increased, and passing beneath the corpora quadrigemina, with which as well as with the cerebellum they make connections, end partly in the region of the optic thalami and walls of the third ventricle, but to a great extent in the cerebral hemispheres. We may in a certain sense consider the rest of the brain as built upon and attached to these fundamental basal or ventral strands.

§ **604**. Connected with the brain are a series of paired nerves, the cranial nerves. The first and second pair, the olfactory nerves and the optic nerves, differ in their origin and mode of development from all the rest so fundamentally as to cause regret that they are included in the same category. We shall consider these by themselves in due course. The remaining pairs, from the third pair to the twelfth, forming a much more homogeneous category, we shall also consider in their proper place. We must now turn to study in greater detail some of the structural features of the brain, and we may with advantage begin with the bulb.

SEC. 2. THE BULB.

§ **605**. The spinal cord, as it ascends to the brain, becomes changed into the more complex bulb, partly by a shifting of the course of the tracts of white fibres, partly by an opening up of the narrow central canal into the wide and superficial fourth ventricle, but chiefly by the development of new grey matter.

When the anterior, ventral, aspect of the bulb is examined (Fig. 108, C), it will be seen that the anterior columns of the cord are interrupted for some distance in the median line by bundles of fibres (*Py. dec*) which, appearing to rise up from deeper parts, cross over from side to side and so confuse the line of the anterior fissure. This is the *decussation of the pyramids,* above which the place of the anterior columns of the spinal cord is taken by two larger, more prominent columns, the *pyramids* of the bulb (*Py.*), which are continued forwards to the hind margin of the pons. On the outer side of, lateral to, each pyramid, lies a projecting oval mass, *the olivary body* or *inferior olive* (*ol.*) separating the pyramid from a column of white matter, *the restiform body* (*R*), which, occupying the lateral region of the bulb, when traced backwards appears to continue the line of the lateral column of the cord, and when traced forwards is seen to run up to the cerebellum as the inferior peduncle of that organ. On the posterior dorsal aspect no such decussation is seen. The two posterior columns of the cord diverge from each other, leaving between them a triangular space, the *calamus scriptorius,* which is the hind part of the lozenge-shaped shallow cavity of the fourth ventricle. As the cord passes into the bulb the posterior column as a whole grows broader, and the division into a median posterior and an external posterior column becomes very obvious and distinct by the appearance of a conspicuous furrow separating the two. At some distance however in front of the point of divergence of the columns or apex of the calamus scriptorius, the furrow becomes less marked, and it eventually fades away. In its course the furrow takes such a line that the median posterior column, forming the immediate lateral boundary of the fourth ventricle,


A
B
C
114
113
112
111
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6
5
4
3
2
1
Pn
Qa
Qp
Pvr.
Cgm
IV
P
SP
P'
SP'
Vla
lc
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4
str
R
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Ac
sp.ac
ep
mp
p.r.Ci.
lat.col
post. col.
Op
III
Cgl
P.vr
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CR
F
Vα
Vβ
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VII
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ol
Py
f.a.e.
ant.col
lat.col
Cm
Po
IX
X
XI
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De
AC
ar.C.i
ant.col

FIG. 108. OUTLINES OF PARTS OF THE BRAIN. A. DORSAL. B. LATERAL. C. VENTRAL ASPECT. (Nat. size). (Sherrington.)

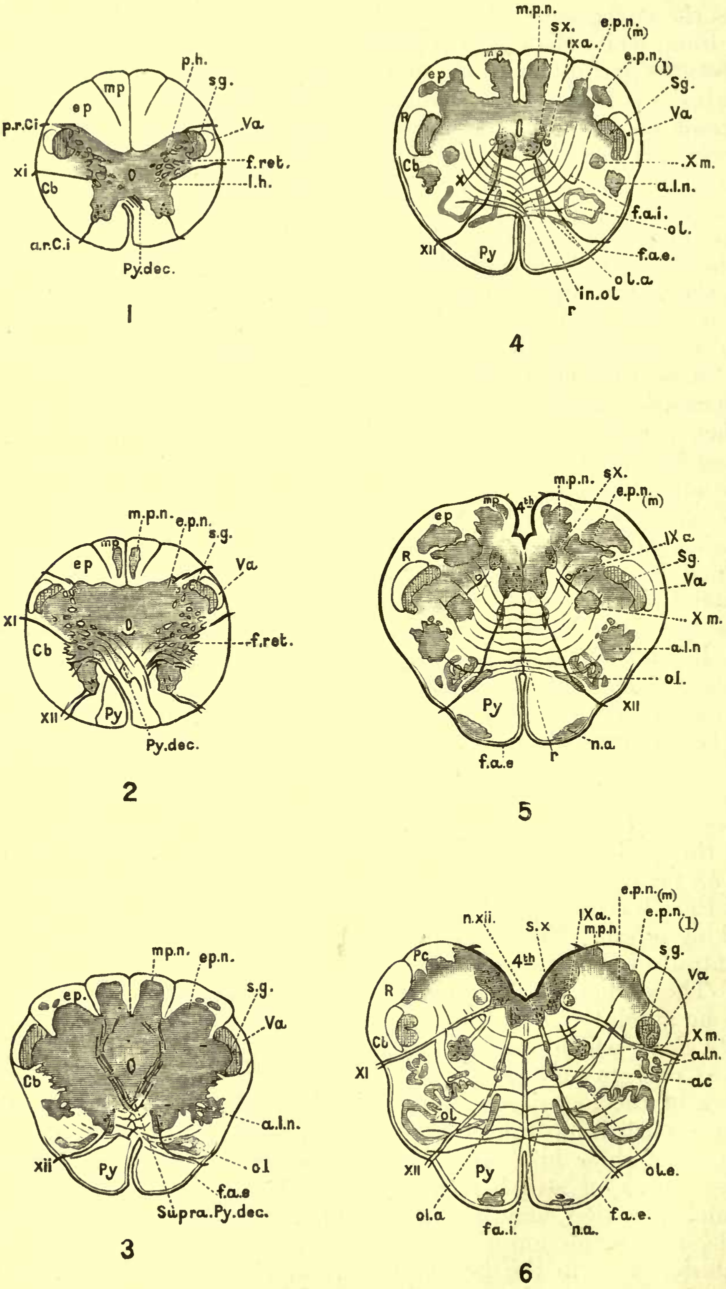
ant. col. anterior, *lat. col.* lateral, *post. col.* posterior column of spinal cord. *m. p.* median posterior column (fasciculus gracilis). *e. p.* external posterior column (fasciculus cuneatus). *Py. de.* Decussation of pyramids. *Py.* pyramid. *ol.* olivary body. *A. c.* ala cinerea. *T. ac.* tuberculum acusticum. *str.* striæ acusticæ. *E. t.* eminentia teres. *F. a.* fovea anterior. *l. c.* locus cæruleus. *f. a. e.* external arcuate fibres. *Vla.* valve of Vieussens. *R.* restiform body. *Po.* pons. *S. P.* superior peduncle, *P.* part of middle peduncle of cerebellum, *SP'. P'.* the same two peduncles cut across; in *B* the limits of each are marked by dotted lines cut across. *CR.* crus cerebri. *Q. P.* posterior, *Q. A.* anterior corpus quadrigeminum. *F.* lateral fillet. *Op.* optic tract. *C. g. l.* lateral, *C. g. m.* median corpus geniculatum. *Pvr.* pulvinar of optic thalamus. *P. n.* pineal gland. *c. m.* corpora mammillaria or albicantia. *p. r. C.* 1. posterior roots, *a. r. C.* 1. anterior roots of first cervical nerve. *sp. ac.* spinal roots of spinal accessory. XII. to III. cranial nerves. V. *a.* motor root, V. *β.* sensory root of fifth. 4. fourth ventricle.

The transverse lines indicate the levels of the sections in Figs. 109—114.

has the appearance of a strand broad behind but thinning away in front, while the external posterior column, also broadening as it advances forwards, seems to be wedged in between the median posterior column on its median edge and the restiform body on its lateral edge; hence the former is here called the *fasciculus* (or *funiculus*) *gracilis* (*m. p.*), and the latter the *fasciculus* (or *funiculus*) *cuneatus* (*e. p.*). Further forward both columns seem to merge with each other and with fibres which curve round to form part of the restiform body; the relations however of these two columns to each other and to the other parts of the bulb, as well as the nature of the other several changes by which the cord is transformed into the bulb, are disclosed by transverse vertical (dorso-ventral) sections, to the study of which we must now turn.

A section (Fig. 109, 1) taken at the hind margin of the decussation, at which level the first cervical nerve takes origin, when compared with a section of the cord at the level of the second cervical nerve (Cf. Fig. 104, C_2), shews that certain changes are already taking place in the grey matter. The anterior horns are not much altered, but the posterior horns are, as it were, pushed out laterally and dorsally so that the posterior columns, which as yet retain their previous great depth, become very much broader than they are lower down, encroaching, so to speak, on the lateral columns. At the same time the substance of Rolando (*s. g.*), forming the head or caput of the horn, has enlarged into a more or less globular form, and lies near the surface of the cord though separated from it by a compact tract of longitudinal fibres (*V. a.*), which as we shall see, belongs to the fifth cranial nerve. A considerable development of the reticular formation (*f. ret.*) at the side of the grey matter ventral to the posterior horn has also taken place, and this with the shifting of the position of the posterior horn has driven the lateral horn (*l. h.*) nearer to the anterior horn. From this lateral horn a root of the eleventh spinal accessory cranial nerve (XI), may be seen taking origin. Further, a great increase of grey matter round the central canal may also be observed.

These changes, however, are of degree only; what seems to be an absolutely new feature is the presence of bundles of fibres (*Py. dec.*), which starting from the anterior column of one side cross over to and are apparently lost in the grey matter of the neck of the anterior horn of the other side; in so crossing the fibres push aside the bottom of the anterior fissure. When the course of these fibres is investigated, either by simple microscopic observation, or still better by the method of degeneration, it is found that they may be traced from the anterior column of one side, across the anterior commissure, through the neck of the anterior horn to the lateral column of the opposite side, and to that part of the lateral column which we have previously described as the crossed pyramidal tract.


1
p.h.
s.g.
mp
ep
p.r.Ci
Va
f.ret.
xi
l.h.
Cb
a.r.C.i
Py.dec.
4
m.p.n.
sx.
e.p.n.(m)
IXa.
e.p.n.(1)
Sg.
mp
ep
Va
R
Xm.
Cb
a.l.n.
f.a.i.
ol.
XII
Py
f.a.e.
ol.a
in.ol
r
2
m.p.n.
e.p.n.
s.g.
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Va
XI
Cb
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XII
Py
Py.dec.
5
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3
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s.g.
ep.
Va
Cb
a.l.n.
xii
Py
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Supra.Py.dec.
6
e.p.n.(m)
n.xii.
s.x
IXa.
m.p.n
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s.g.
Pc
4th
Va
R
Xm.
Cb
a.l.n.
XI
ac
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XII
Py
ol.e.
ol.a
fa.i.
n.a.
f.a.e.

Fig. 109. Transverse Dorsoventral Sections of the Bulb (Man) at Different Levels. (Sherrington.)

This and Figs. 110—114, form a series of transverse dorsoventral sections of the brain taken at different levels from the hind end of the bulb to the front of the third ventricle; the several levels are shewn by the lines drawn in Fig. 108. They are all magnified twice. The details are shewn, for the sake of simplicity, in diagrammatic fashion; the white matter is left unshaded, the course of the fibres being indicated in a few important instances only; the grey matter is shaded formally, the nerve-cells being indicated in the case only of the nuclei of the cranial nerves. The want of complete bilateral symmetry which is often met with in such sections is indicated in several of the figures.

1. At the hind limit of the decussation of the pyramids. 2. In the middle of the decussation. 3. At the upper end of the decussation. 4. Just below the point of the calamus scriptorius. 5. Just above the point. 6. Through the middle of the ala cinerea.

Py. Pyramids. *Py. dec.* decussation of the pyramids. *Supra Py. dec.* superior decussation. *f. a. i.* internal arcuate fibres. *f. a. e.* external arcuate fibres. *Cb.* position of cerebellar tract. *R.* restiform body or inferior peduncle of the cerebellum. *e. p.* external posterior column, fasciculus cuneatus, *m. p.* median posterior column, fasciculus gracilis. *r.* raphe.

l. h. lateral horn. *m. p. n.* nucleus of the median posterior column or gracile nucleus. *e. p. n.* nucleus of the external posterior column or cuneate nucleus. *e. p. n.* (*m.*) median division and *e. p. n.* (*l.*) lateral division of the same. *ol.* olivary body. *ol. a.* median accessory, and *ol. e.* lateral accessory olive. *in. ol.* interolivary layer. *a. l. n.* lateral (antero-lateral) nucleus. *n. a.* arcuate nucleus. *a. c.* remnant of anterior horn. *f. ret.* reticular formation. *s. g.* substance of Rolando.

a. r. c. I. anterior root, and *p. r. c.* I. posterior root of first cervical nerve. XI. root of spinal accessory nerve. XII. twelfth or hypoglossal nerve. *n.* XII. nucleus of the same in 6; the nucleus may be traced however through 2, 3, 4, 5, in connection with the fibres of the nerve. *s.* X. sensory or main part of the glossopharyngeal-vago-accessory nucleus. X. *m.* motor nucleus of the vagus, or nucleus ambiguus. IX. *a.* ascending root of the glossopharyngeal nucleus. V. *a.* ascending root of the fifth nerve.

4th. fourth ventricle; the ependyma or lining is indicated by a thick dark line; and in 5 and 6, the tooth-like section of the projecting obex is shewn.

In a section a little higher up (Fig. 109, 2), these decussating fibres form on each side a large strand which starts from a part of the anterior column, now becoming distinctly marked off as the pyramid (*Py.*), and is apparently lost in the reticular formation, but in reality passes on to the crossed pyramidal tract of the lateral column. This strand, as it crosses over, completely cuts off the head of the anterior horn from the more central grey matter, and forms with its fellow a large area of decussating fibres between the bottom of the anterior fissure and the central grey matter. When a surface view of the bulb is examined the decussation is seen to be effected by alternate bundles, passing now from right to left, now from left to right; and in transverse sections we find correspondingly that the anterior fissure appears bent now to the left and now to the right, according as the section cuts through a bundle passing from left to right or from right to left.

In sections still higher up (Fig. 109, 3 and 4) this conspicuous strand of fibres crossing obliquely from side to side, will be no longer seen; decussating fibres are seen dorsal to the anterior fissure, but these, of which we shall speak presently, are of different nature and origin. The fibres which in sections below were seen in the act of crossing are now gathered into masses of longitudinal fibres, the pyramids, (*Py.*) one on each side of the anterior fissure, each with a sectional area of a rounded triangular form clearly marked out from the surrounding structures; the section is taken above the decussation of the pyramids. Or, tracing the changes from below upwards we may say that the decussation is now complete; on each side the whole of the crossed pyramidal tract of the spinal cord has, in the region of the bulb below the level of the present sections, crossed over to the other side, and joining with the direct pyramidal tract of the anterior column of the cord of the same side has become the pyramid of the bulb. In other words, the decussation of the pyramids is, as we have already hinted, the passing off from each pyramid, and the crossing over to the opposite side of the cord, of those fibres which are destined to become the crossed pyramidal tract of the spinal cord of the opposite side, while the rest of the pyramid pursues its course on the same side as the direct pyramidal tract.

§ **606.** In the spinal cord the bottom of the anterior fissure is separated from the central canal by nothing more than the anterior white commissure and a narrow band of grey matter, composed of the anterior grey commissure and of part of the central gelatinous substance. During the decussation of the pyramids, the decussating fibres push, as it were, the central canal with its surrounding grey matter to some distance from the bottom of the anterior fissure. In sections above the decussation the bottom of the fissure does not again approach the central canal, but continues to be removed to some distance from it, and, as we pass upwards, to an increasing distance, by the interposition of tissue which consists largely of decussating fibres. These however, though they seem to continue on the decussation of the pyramids, are shewn by the embryological and degeneration methods to have no connection with the pyramids, but to belong to another system of decussation. As we have seen (§ 565) the anterior commissure along the whole length of the cord contains decussating fibres. Some of these in the upper part of the cord are fibres crossing from the direct pyramidal tract of one side to the grey matter of the other side, and so may be regarded as part of the whole pyramidal tract; but others are of different origin; and even in the region of the actual decussation of the pyramids some of the fibres which cross over do not belong to the pyramidal tract. This system of decussating fibres becomes increasingly prominent above the decussation of the pyramids, and through it the ventral area of the bulb between the central canal and the anterior fissure is much increased. The fibres as they cross form a middle line of partition, the *raphe* (Fig. 109, 4, 5, *r*), which increases in depth in the upper parts of the bulb, and on each side of the raphe help to break up the grey matter (which previously formed the anterior horns) into what is called the *reticular formation.* We shall return to this presently, but may here call attention to a special development of these decussating fibres which is seen just above the decussation of the pyramids. In a section at this level (Fig. 109, 3) a strand of fibres (*supra Py. dec.*) may be seen to start chiefly from the gracile nucleus but also to some extent from the cuneate nucleus, to sweep round the central grey matter, and to decussate ventral to this between it and the bottom of the anterior fissure. This is called the *superior decussation*, or, for reasons which we shall see later on, the *sensory decussation.*

§ **607.** We must now turn to the posterior fissure and its relations to the fourth ventricle. We saw that at the beginning of the pyramidal decussation, the posterior horns had been thrown backwards and outwards so as to increase the posterior columns. The posterior fissure is still of great depth, so that by the increase of breadth and maintenance of depth the posterior column, the lateral limit of which is still sharply marked out by the swollen head of the posterior horn as well as by the highest posterior rootlets of the first cervical nerve, acquires at this level its maximum of bulk.

From this point forward the depth of the posterior fissure and the dorso-ventral diameter of the posterior columns diminishes. The head of the horn (Fig. 109, 2) is thrown still further outwards into the lateral regions; developments of grey matter at the base and to some extent at the neck of the horn (of these we shall speak presently) encroach (Fig. 109, 3) dorsally on the white matter of the columns; and the central grey matter appears to rise dorsally at the expense of the posterior fissure, in coincidence with the development described above as taking place on the ventral side of the canal.

Still a little further forward, in a section for instance (Fig. 109, 4) a little way behind the apex of the *calamus scriptorius,* the central grey matter, which still forms a rounded mass around the central canal, is brought yet nearer to the posterior fissure.

In a section yet a little further forward (Fig. 109, 5) carried through the hinder narrow part of the fourth ventricle itself, it is seen that the central canal has opened out on to the dorsal surface, and that the grey matter, which in previous sections surrounded it, is now exposed to the surface on the floor of the ventricle, the median posterior columns being thrust aside. In a still more forward section (Fig. 109, 6) this grey matter in correspondence with the increasing width of the ventricle occupies a still wider area, thrusting still further aside the narrowing upper ends of the two posterior columns.

During these successive changes, the large wide posterior (both external posterior and median posterior) columns of the cervical spinal cord and beginning bulb, are reduced to small dimensions and in the end disappear; but before we speak of the course and fate of the tracts of fibres constituting these columns we must turn to the important changes of the grey matter.

§ 608. A transverse section through the lower end of the decussation (Fig. 109, 1) shews, as we have said, few differences as regards the grey matter from one taken at the level of the second cervical nerve. The changes noticeable are mainly the changes in position of the posterior horns, the increase of central grey matter around the central canal, the approach of the lateral horn, from which spring the roots of the spinal accessory nerve, to the anterior horn, and an increase of the reticular formation in the bay ventral to the posterior horn.

In the middle of the decussation (Fig. 109, 2) the decussating fibres are cutting the head of the anterior horn away from the base of the horn and the central grey substance, and the isolated head is diminishing in size, being separated from the surface of the cord by an increasing thickness of white matter. The lateral horn and origin of the spinal accessory root do not share in this isolation, but are driven back again dorsally towards the posterior root to join the reticular formation which is increasing in area, while the lateral column of white matter is diminishing in bulk by the withdrawal of the pyramidal tract.

Still a little further forward, the anterior horn seems at first sight to have wholly disappeared (Fig. 109, 3 and 4), but its disappearance is coincident with an increase of the reticular formation in the position of the lateral columns, as well as with the growth of tissue mentioned above between the anterior fissure and the central grey matter. In fact, between the anterior pyramids on the ventral side and the largely increased and laterally expanded grey matter on the dorsal side, a large area of peculiar tissue now extends on each side for a considerable distance from the middle line of the raphe, encroaching on what was the lateral column of white matter; and a corresponding area of similar tissue may be traced from this level through the higher parts of the bulb up into the pons and crura cerebri. The tissue consists of nerve fibres running transversely, longitudinally, and in other directions, so as to form a network, the bars of which are often curved; and with these fibres are found branched nerve cells in considerable number, some of them small, both fibres and cells being as elsewhere embedded in neuroglia. Though differing from the ordinary grey matter of the cord by the more open character of its network. it may be considered as a form of grey matter. We may consider it as being in reality the grey matter of the apparently lost anterior horn broken up and dispersed by the passage of a large number of fibres and bundles of fibres, especially of the decussating fibres spoken of in § 606, which since they curve through this area from the middle line laterally are called arcuate or arciform fibres, *internal arcuate fibres* (Fig. 109, 6, *f. a. i.*) to distinguish them from the *external arcuate fibres* (*f. a. e.*) of which we shall speak presently. Fragments of more compact grey matter, also belonging probably to the anterior horn, are seen at intervals in this area, Fig. 109, 6, *ac.* and elsewhere. We have seen that nearly all the way along the cord the grey matter of the neck of the posterior horn is similarly broken up by bundles of fibres into what we there called the reticular formation (Figs. 98, 99, *r. f. p.* and *r. f. l.*); and this area in the bulb though it possesses characters of its own is also called *the reticular formation.* In the more lateral portion of this formation, the network is more open and irregular, the fibres are finer, and the nerve cells are more abundant than in the median portion where the nerve cells, except in the immediate neighbourhood of the raphe, are less numerous or even absent, and the fibres are coarser. These two parts are sometimes distinguished as the outer or lateral, and the inner or median formation. In the middle line the fibres distinctly interlace and decussate in an oblique manner, some running nearly vertically in the dorso-ventral plane, thus constituting as we have said a thick raphe, which, however, at its edges gradually merges into the more open network.

§ **609**. Within the area, bounded by the pyramids ventrally, the expanded grey matter dorsally, the raphe in the middle line, and the white matter laterally, certain distinct compact masses of grey matter make their appearance, as we pass upward towards the pons.

One of the most important of these gives rise to the *olivary body*, or *inferior olive* which, as we have seen, projects as an oval mass (Fig. 108, *ol.*) on each side of the pyramids, reaching from a level which is somewhat higher up than the lower limit of the pyramids, almost but not quite to the pons. The olivary body, as a whole, consists partly of white matter, that is of fibres, and partly of grey matter, sometimes called the *olivary nucleus.* This latter is disposed in the form of a hollow flask or curved bowl, with deeply folded or plaited walls, having a wide open mouth directed inwards towards the middle line, and forwards towards the pons (Fig. 109, 4, 5, 6, *ol.*). The flask is filled within by white matter, and covered up on its outside with white matter as well as traversed by fibres. The grey matter thus forming this flask-shaped nucleus consists of small rounded nerve cells, lying in a bed of tissue which is partly ordinary neuroglia, and partly a fine nervous network.

Lying to the median side of the olivary body, immediately dorsal to the anterior pyramid is another small mass of grey matter, in the form of a disc, appearing in transverse sections as a thick bent rod, in some sections consisting of two parts (Fig. 109, 4, *ol. a*). This is the *accessory olivary nucleus.* A very similar body lies dorsal to the olivary nucleus, in the lateral reticular formation; this is also called an accessory olivary nucleus, being distinguished (Fig. 109, 6, *ol. e*) by the name *outer accessory* nucleus from the above mentioned *inner accessory* nucleus. It will be observed in these transverse sections that the inner accessory nucleus is separated from the olivary nucleus by a bundle of white fibres (Fig. 109, 4, 5, 6, XII) which, running ventrally from the grey matter in the dorsal region, comes to the surface between the anterior pyramids and the olivary body. This is the hypoglossal or twelth cranial nerve.

On the surface of the anterior pyramid itself is seen on each side a small mass of grey matter (Fig. 109, 5, 6, *n. a.*), which since it appears to be connected with a system of superficial transverse fibres, which we shall describe directly as the *external arcuate fibres* (Fig. 109, 3, 4, 5, 6, *f. a. e.*), is called the *arcuate nucleus.* It seems to belong to the same group as the accessory olives.

Lastly, a small somewhat diffuse collection of grey matter is seen in sections as a rounded mass of irregular form placed lateral to the reticular formation (Fig. 109, 4, 5, 6, *a. l. n*). This, which at its first appearance seems to be budded off from the general mass of grey matter (Fig. 109, 3, *a. l. n*) and which is probably a detached portion of the base of the anterior horn or of the lateral region of the grey matter, is called the *lateral* or *antero-lateral* nucleus.

Hence, besides the diffuse reticular formation, this ventral part of the bulb contains more sharply defined collections of grey matter in the olivary nucleus, and the other bodies just mentioned.

§ **610**. We must now turn to the dorsal part of the bulb. Here in the first place we must distinguish between the portions of grey matter which are more immediately connected with the cranial nerves taking origin from this part of the bulb, and the portions which have no such obvious connection. In the spinal cord, the anterior horns supply, as we have seen, the origins of the successive anterior motor nerves; but in the transformation of the cord into the bulb the anterior horns have been broken up or displaced; and the parts of the anterior horns, serving as the nuclei of origin for motor nerves, have been translated from the ventral to the more dorsal regions. Hence, it is in the more dorsal part of the grey matter that we have to seek for the nuclei of origin not only of afferent but also of motor cranial nerves. It will be convenient to consider all these nuclei of origin of cranial nerves by themselves, and we may here confine ourselves to the grey matter of other nature. We may however say that these nuclei from that of the third nerve backwards are more or less closely associated with the grey matter immediately surrounding the central canal. This *central grey matter*, in the narrow sense of the term, is marked out somewhat low down

(Fig. 109, 3) by the fibres of the sensory decussation which sweep round it; it appears in sections higher up as a fairly distinct region (Fig. 109, 4); and it is this part of the grey matter which is exposed on the floor of the fourth ventricle when the central canal (Fig. 109, 5, 6) opens out into that space. We say exposed; but in reality the true grey matter is covered by a superficial layer of tissue of a peculiar nature (indicated in Fig. 109, 5, 6, by a thick black line) similar to that which is found at the hind end of the conus medullaris in the spinal cord.

We saw that at the level of the first cervical nerve coincident with the horizontal flattening out of the posterior horns the posterior columns assumed very large dimensions. In this region (Fig. 109, 1) they consist entirely of white matter, that is, of longitudinal fibres.

At a little higher level, however, at the level of the middle of the decussation for example, an islet of grey matter (Fig. 109, 2, *m. p. n.*) makes its appearance in the median posterior column. A little further forward, at the level of the established pyramids, it will be seen (Fig. 109, 3) that this islet is the hind end of an invasion from the more centrally placed grey matter, and that at the same time there has taken place a similar inroad of grey matter into the external posterior column (Fig. 109, 3, *e. p. n.*); indeed a slight extension of grey matter into the external posterior column may be seen even before this (Fig. 109, 2, *e. p. n.*). It will further be observed that these grey masses have so largely encroached on the white matter, that both the median posterior or fasciculus gracilis and the external posterior column or fasciculus cuneatus, instead of being simply tracts of white fibres as they were in the hinder part of the bulb and in the cord, have now become columns of grey matter covered by a relatively thin layer of white fibres. These columns of grey matter are now called respectively the *median posterior nucleus*, or *nucleus fasciculi gracilis*, or more shortly, the *gracile nucleus;* and the *external posterior nucleus*, or *nucleus fasciculi cuneati*, or the *cuneate nucleus.* From the ventral aspect of these nuclei a large number of fibres pass ventrally with a more or less curved course to form as we have seen, § 606, the superior decussation and to pursue certain paths through the reticular formation, of which we shall speak later on. It is at this level and for some little distance above (Fig. 109, 4, 5), that these nuclei acquire their greatest development. Farther forward (Fig. 109, 6), when the fourth ventricle has opened out and the nuclei of the cranial nerves are becoming conspicuous, and the posterior columns have been thrust aside laterally, both these nuclei have diminished in size; still farther forward they become still smaller, and towards the pons they gradually disappear.

The mass of gelatinous substance, forming at the level of the first cervical nerve the swollen caput of the horn close to the surface but separated from it by a band of fibres (*Va*) of fine calibre, to which we have already referred as belonging to the fifth cranial nerve, increases in bulk at a somewhat higher level, Fig. 109, 2, 3, *s.g.*, and forms on the surface a slight projection, called *the tubercle of Rolando.* It soon, however, becomes thrust ventrally by the divergence of the posterior columns, and more and more covered up by the fibres which are going to form the increasing restiform body, Fig. 109, 4, 5, 6, *R.* Retaining this position the islet of gelatinous substance diminishes in size farther forwards, Fig. 110, *s.g.*, and eventually disappears.

§ **611.** *The Fibres of the Bulb.* It is obvious, from what has already been said, that the arrangement into posterior, lateral and anterior columns, so clear and definite in the spinal cord, becomes broken up in the bulb; indeed it will be best in treating of the bulb, not to attempt to trace out these columns, but to speak of the course of the several tracts into which these columns may be divided.

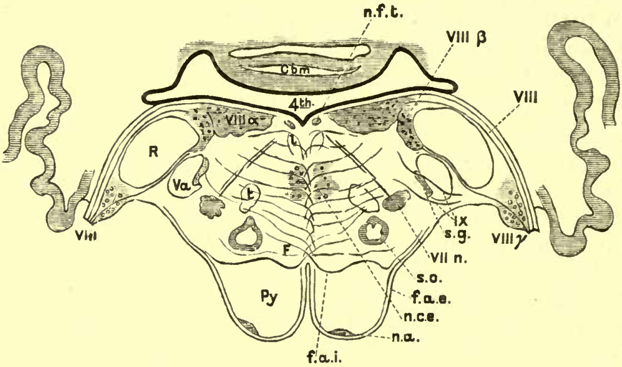

Fig. 110. Through the Bulb just behind the Pons. (Sherrington.)
Taken in the line 110, Fig. 108.

Py. Pyramids. *R.* Restiform Body. *Cbm.* cerebellum. *F.* Fillet. *f. a. e.* external, *f. a. i.* internal arcuate fibres. *t.* bundle of fibres from olive to the lenticular nucleus. *l.* posterior longitudinal bundles. *n. f. t.* nucleus of fasciculus teres. *s. o.* superior olive. *n. c. e.* nucleus centralis (the marks within it are sections of bundles of fibres by which it is traversed). *s. g.* substance of Rolando.

V. *a.* ascending root of fifth nerve. VII. *n.* nucleus of the 7th nerve. VIII. auditory nerve, chiefly the dorsal or cochlear root; VIII. *a.* median nucleus, VIII. *β.* lateral nucleus, VIII. *γ.* accessory nucleus of auditory nerve. IX. fibres of root of ninth nerve passing through ascending root of fifth nerve.

The direct and crossed pyramidal tracts of the cord unite to form, as we have seen, the pyramid of the bulb, and so pass on to the pons. We need say nothing more at present concerning this important pyramidal strand except that, as we trace it down from the pons to the spinal cord, it gives off to the bulb itself fibres which make connections with the motor fibres of the cranial nerves proceeding from this region.

Concerning the course taken by the other less conspicuous "descending" tract, the antero-lateral descending tract, our knowledge is very imperfect; nothing definite can be said at present.

The cerebellar tract, occupying near to the surface a position which in the series of sections (Fig. 109, *Cb*) appears now rather more ventral now more dorsal, eventually passes into the restiform body, of which it forms a large part, and thus reaches the cerebellum. The antero-lateral ascending tract possibly also takes the same course, but this is not as yet certain.

The median posterior tract or column, becoming the fasciculus gracilis, ends in the gracile nucleus; and in a similar manner the external posterior column, or fasciculus cuneatus, ends in the median and lateral masses of the cuneate nucleus. As we have seen, the white matter of these columns diminishes as the nuclei increase; and the nuclei after absorbing, so to speak, the white matter diminish in turn; the ascending degeneration observed in these columns stops at these nuclei. It is a suggestive fact that as these nuclei diminish forwards the restiform body increases in bulk.

The remaining fibres of the cord, belonging partly to the anterior column and partly to the lateral column, not gathered into any of the above mentioned tracts, appear to end chiefly at all events in the reticular formation of the bulb itself, though some are carried on to the higher parts of the brain.

§ **612**. Thus of the various tracts or strands of the spinal cord two only are known definitely and certainly to pass as conspicuous unbroken strands through the bulb to or from higher parts; namely, the pyramidal tract to the cerebrum and the cerebellar tract to the cerebellum. All or nearly all the rest of the longitudinal fibres of the cord reaching the bulb end, as far as we know at present, in some part or other of the bulb; and we may infer that some or other nerve cells of the bulb serve as relays to connect these fibres of the cord with other parts of the brain.

The gracile and cuneate nuclei stand out conspicuously as relays of this kind, and through them the posterior columns of the cord make secondary connections on the one hand with the cerebellum and on the other hand with various regions of the cerebrum. We have said § 606 that fibres passing ventrally from the gracile and cuneate nuclei sweep in a curved course through the reticular formation as the internal arcuate fibres (Fig. 109, *f. a. i.*). The hindmost of these form the superior decussation already referred to as seen in sections at the fore-part of and in front of the pyramidal decussation (Fig. 109, 3, *supra Py. dec.*). After decussating ventral to the central canal these fibres form an area called the *inter-olivary layer* (Fig. 109, 4, *in. ol.*) lying dorsal to the pyramids between the two olivary nuclei. This layer may be regarded as the hind end or beginning on each side of a remarkable longitudinal strand called the *fillet* (Figs. 108, *B. F.*, 110, *F.*)

of the connections of which in the front part of the brain we shall speak hereafter. Thus these two nuclei are the source of fibres which cross to the other side of the bulb, and reaching the inter-olivary layer dorsal to the pyramids run up to higher parts of the brain by the fillet. We may add that the formation of the fillet is also probably assisted by fibres from a tract which lies just dorsal to the interolivary layer and is derived from the anterior columns of the cord. Besides its fibres of descending degeneration the anterior column contains fibres of ascending degeneration, and these rise dorsally in the bulb to form the tract in question. Though the whole tract is of some length, the component fibres appear to be short.

The gracile and cuneate nuclei give rise also to other fibres which, though also sweeping ventrally and crossing to the other side, do not, when they reach the inter-olivary region, assume a longitudinal direction as do the fibres forming the fillet, but as external arcuate fibres (Fig. 109, *f. a. e.*) pursue a course which is at first ventral along the side of the anterior fissure and then lateral over the ventral surface of the pyramid and olivary nucleus, by which path they reach the lateral surface of the bulb, and so the restiform body and cerebellum. In this way, the two nuclei in question contribute to the restiform body of the opposite side of the bulb. These external arcuate fibres, which as they sweep round the ventral surface of the pyramid traverse the arcuate nucleus, though they vary much in individual brains, form a considerable portion of the white matter seen on the ventral and lateral surfaces of the bulb; it is by them that the olivary nucleus is covered up.

The cuneate and gracile nuclei, besides this crossed and somewhat roundabout connection with the restiform body of the opposite side, are believed to have more direct connection with the restiform body of the same side by means of fibres which pass by a more or less direct lateral path from them to it. Accepting this view we may say that the two nuclei are connected with the opposite side of the cerebellum by external arcuate fibres, and with the same side of the cerebellum by the other fibres just mentioned. In any case the connection between the two nuclei and the cerebellum is large and important.

Thus the important strand of fibres which is called in the bulb the restiform body, and higher up the inferior peduncle of the cerebellum, is connected with the spinal cord in two chief ways: directly by means of the cerebellar tract, and indirectly by means of the cuneate and gracile nuclei which, as we have said, diminish in bulk forwards as the restiform body increases. By the relay of the gracile nucleus it is brought into connection with the median posterior column along the whole length of the cord, and so with that division of the posterior roots which (§ 577) in each of the several spinal nerves goes to form that column. By the relay of the cuneate nucleus it is brought into connection with such parts of the external posterior column as end in that nucleus, and thus probably with other fibres of the posterior roots of the upper spinal nerves. And if we admit that the cerebellar tract is connected, by the relay of the vesicular cylinder or by other nerve cells, with the rest of the posterior roots of the spinal nerves, we may conclude that the restiform body is, by means of these relays, a prominent continuation of all the spinal posterior roots.

The restiform body and so the cerebellum is also specially connected with the olivary body of the opposite side; for when in young animals one side of the cerebellum is removed the olivary body of the opposite side atrophies. The course of the fibres maintaining this connection is not as yet accurately known, but they probably pass from the olivary nucleus of one side through the interolivary layer and so laterally through the reticular formation of the other side. Lastly we may add that a tract which is sometimes included in the restiform body as its median or inner division has quite a different origin from any of the above; the fibres which compose it come, as we shall see, from the auditory nerve.

The further connections of the bulb with the cerebrum it will be best to leave until we come to deal with the structural arrangement of the rest of the brain.

Meanwhile enough has been said to shew that the bulb differs very materially in structure from the spinal cord. The grey matter of the bulb is far more complex in its nature than is that of any part of the cord; and the arrangement of the several strands and tracts of fibres is far more intricate. The structural features on the whole perhaps suggest that the main functions of the bulb are twofold; on the one hand it seems fitted to serve as a head centre governing the spinal cord, the various reins of which, with the exceptions noted, it holds as it were in its hands; on the other hand it appears no less adapted to act as a middleman between parts of the spinal cord below and various regions of the brain above. As we shall see experiment and observation give support to these suggestions.

SEC. 3. THE DISPOSITION AND CONNECTIONS OF THE GREY AND WHITE MATTER OF THE BRAIN.

The Grey Matter.

§ **613**. As we pass up from the bulb to the higher parts of the brain, the differentiation of the grey matter into more or less separate masses, which we have seen begin in the bulb, becomes still more striking. We have to distinguish a large number of areas or collections of grey matter more or less regular in form and more or less sharply defined from the surrounding white matter; to such collections the several terms corpus, locus, nucleus and the like have from time to time been given. These areas or collections vary greatly in size, in form and in histological characters; they differ from each other in the form, size, features and arrangement of the nerve cells, in the characters of the nervous network of which the nerve cells form a part, and especially perhaps in the extent to which the more distinctly grey matter is traversed and broken up by bundles of white fibres. Guided by the analogy of the spinal cord, as well as by the results of experiments and observations directed to the brain itself, we are led to believe that the complex functions of the brain are intimately associated with this grey matter; and a full knowledge of the working of the brain will carry with it a knowledge of the nature and meaning of the intricate arrangement of the cerebral grey matter. At present, however, our ignorance as to these things is great; and, though various theoretical classifications of the several collections of grey matter have been proposed, it will perhaps be wisest to content ourselves here with a very broad and simple arrangement. We will divide the whole grey matter of the brain into four categories only. 1. The central grey matter lining the neural canal; and with this we may consider the nuclei of the cranial nerves some of which are closely associated with it. 2. The superficial grey matter of the roof of some of the main divisions of the brain, such as that of the cerebral hemispheres, and of the cerebellum. 3. The intermediate grey matter more or less closely connected with the crura cerebri. 4. Other collections and areas of grey matter. We will, moreover, confine ourselves at present for the most part to their general features and topography, reserving what we have to say concerning their histological characters for another occasion.

1. *The Central Grey Matter, and the Nuclei of the Cranial Nerves.*

§ **614**. The ventricles of the brain like the central canal of the spinal cord, of which they are a continuation, are lined by an epithelium which is in general a single layer of columnar cells said to be ciliated throughout, though it is often difficult to demonstrate the cilia. Beneath this epithelium lies a layer of somewhat peculiar neuroglia, forming with the epithelium, as we have said (§ 610), the *ependyma*, which, well developed in the floor of the fourth ventricle and in the walls of the third ventricle, and of the aqueduct, is thin and scanty in the lateral ventricles. Beneath, and more or less connected with the ependyma in the sides and floor of the third ventricle, is a fairly conspicuous layer of grey matter, which is well developed in the parts of the floor exposed on the ventral surface of the brain, and known as the lamina terminalis, the anterior and posterior perforated spaces, the tuber cinereum &c. This layer is not continued forwards into the lateral ventricles of the cerebral hemispheres, but it is well-developed backwards along the aqueduct (Figs. 113, 114) and in the floor of the fourth ventricle, and through the bulb becomes, as we have seen (§ 610), continuous with the central grey matter of the cord. The nerve cells of this grey matter are on the whole small and in many places scant.

§ **615**. The several roots of the cranial nerves from the third nerve backwards may be traced within the brain substance to special collections of grey matter, called the *nuclei of the cranial nerves*, some of which lie close upon the central grey matter, while others are placed at some distance from it. The optic nerve and what is sometimes called the olfactory nerve, namely, the olfactory bulb and tract, may advantageously be dealt with apart, since these two nerves are not, like the other cranial nerves, simple outgrowths from the walls of the original neural canal, but are in reality elongated vesicles, budded off from the neural canal, the cavities of which have been obliterated. We may add that part of the retina, and of the grey matter of the olfactory tract, may perhaps be considered as corresponding to the nuclei of which we are speaking, the retinal and proper olfactory fibres being connected with them very much as the fibres of the remaining cranial nerves are connected with their respective nuclei.

In the brain, the segmental regularity of the nerve roots so conspicuous in the spinal cord is very greatly obscured. We shall have something to say on this point later on; but at present we may be content to treat the several nerves in a simple topographical manner. They may be seen in a ventral view of the brain Fig. 108, C leaving the brain at various levels by what is called their "superficial origin;" the third nerve issuing in front of the pons, and the last or hypoglossal stretching back to the hind end of the bulb. Part, indeed, of the eleventh nerve, the spinal accessory nerve properly so called, makes connections with the spinal cord below the bulb as far back as the sixth or seventh cervical nerve, or even lower; but this part may by these connections be distinguished from the remaining part of the nerve, as well as from all the other cranial nerves. The nuclei to which the nerve roots may be traced within the brain substance, sometimes spoken of as the "deep origin," range in position from the hinder part of the bulb to the hind end of the third ventricle. The nucleus of the hypoglossal nerve begins in the bulb just above the decussation of the pyramids, the nucleus of the third nerve ends beneath the hind end of the floor of the third ventricle; and all the rest of the nuclei may be broadly described as placed between these limits in various parts of the floor of the central canal or in adjoining structures, though part of one nucleus, namely, that of the fifth nerve, can be traced, as we shall see, back into the spinal cord as far as the second cervical nerve and probably extends still farther. Fig. 115 is a diagram shewing in a roughly approximate manner the nuclei of the several nerves as they would appear in a bird's-eye view of the floor of the aqueduct and fourth ventricle looked at on the dorsal aspect.

§ **616.** *The Twelfth* or *Hypoglossal Nerve.* The nucleus of this nerve, which it will be convenient to take first (Fig. 115, XII.), is a long column of grey matter lying in the bulb parallel to, and very close to, the median line. It reaches from the hinder part of the fourth ventricle, at about the level of the hind end of the auditory nucleus, as far back as beyond the hind end of the olivary body. At its extreme hind end or beginning (Fig. 109, 2), it occupies a ventral position and is a part of the anterior horn; thence it gradually rises dorsally (Fig. 109, 3, 4, 5), but so long as the central canal remains closed continues to occupy a distinctly ventral position in reference to the central canal; in its front part, it is, by the opening up of the fourth ventricle, brought into an apparently more dorsal position (Fig. 109, 6).

The nucleus consists mainly of large nerve cells with distinct axis-cylinder processes, which though pursuing a somewhat irregular course may be traced into the fibres of the nerve. These, starting from the ventral surface of the nucleus along its length, run ventrally through the reticular formation, and making their way in a series of bundles, between the olivary nucleus on the lateral side and the pyramid and median accessory olive on the median side, gain the surface along the groove which separates the pyramid from the olivary body.

§ **617**. *The Ninth* or *Glossopharyngeal, Tenth* or *Vagus*, and *Eleventh* or *Spinal accessory Nerves.* It will be advantageous to consider these three nerves together.

In the spinal accessory nerve we must distinguish, as we have said, two parts: the "spinal accessory" proper, formed by the roots which come off from the cervical spinal cord, reaching as far down as the sixth or seventh cervical nerve, and the "bulbar accessory," whose roots come off from the bulb just below the vagus.

The spinal accessory proper takes origin in the group of cells lying in the extreme lateral margin of the anterior horn, from whence the fibres proceed directly outwards through the lateral column, and issue from the cord along a line intermediate between the anterior and posterior roots; the upper roots undergo, with the portion of the lateral horn from which they spring, the shifting spoken of in § 605.

The bulbar accessory starts from an elongated nucleus in the bulb which is common to it, to the vagus, and to the glosso-pharyngeal; hence we have taken these three nerves together. This (Fig. 115) stretches farther forward than the hypoglossal nucleus, reaching the level of the transverse fibres called striae acusticae (*str.*), but does not extend so far behind.

In transverse sections of the bulb, which pass a little below and a little above the point of the calamus scriptorius (Fig. 109, 4, 5), two nuclei or collections of cells are seen in the grey matter round the central canal. The more ventral one is the hypoglossal nucleus, the more dorsal one the beginning or hind part of the combined accessory-vago-glossopharyngeal nucleus.

When a little farther forward the central canal opens out into the fourth ventricle (by which change the hypoglossal nucleus (Fig. 109, 6 *n*. XII.) is brought nearer to the dorsal surface in the floor of the fourth ventricle) this combined nucleus, increasing in breadth, is thrown to the side and assumes a more lateral position, lying now on the side of, but still somewhat dorsal to, the hypoglossal nucleus, between it and the now diminishing gracile nucleus. In this position the nucleus appears to consist of two parts, a median and lateral, the median part having conspicuous nerve cells of moderate size, the lateral part having but few cells, and those of small size. From this level the nucleus runs forwards, maintaining nearly the same position in the floor of the fourth ventricle but gradually becoming thinner, and ends as we have said at about the level of the striae acusticae on the dorsal surface corresponding on the ventral surface to a level a little behind the hind margin of the pons.

From this combined nucleus, but chiefly from the median part, fibres sweep in a ventral and lateral direction through the dorsal part of the reticular formation, pass ventral to, or in some cases through the gelatinous substance and the strand of fibres connected with the fifth nerve (Fig. 109, V. *a*), and reach the surface of the bulb on its lateral aspect in a line between the olivary and restiform bodies (Fig. 108, C). Along this line may be seen (Fig. 108, C.) a series of roots; of these the lowest, the accessory roots, spring from the hind part, the highest, the glossopharyngeal roots, from the front part (and it is these especially which pierce the gelatinous substance (Fig. 110, IX. *a*)), and the intermediate, the vagus roots, from the middle part of the combined nucleus. Hence we may speak of the hind part of the whole nucleus as being the accessory nucleus, the middle part as the vagus nucleus, and the front part as the glossopharyngeal nucleus.

All the fibres however of the roots of these three nerves do not take origin from the nucleus in question; some of the fibres start in a different way. In sections of the bulb above the decussation of the pyramid a patch of grey matter is seen lying in the lateral part of the reticular formation (Fig. 109, X. *m*), about midway between the ventral and dorsal surfaces. What is thus disclosed by sections is a column of grey matter, the "nucleus ambiguus" (Fig. 115, *na*), stretching about as far forwards and backwards as the combined accessory-vago-glossopharyngeal nucleus, but placed distinctly more ventrally and somewhat more laterally. (In Fig. 115, it and the combined nucleus are represented on different sides of the diagram, to avoid confusion through the overlapping of the shading.) From it fibres curve round (Fig. 109, 6, X. *m*), to join the accessory-vago-glossopharyngeal roots, but especially the vagus roots. It may therefore be considered as a second nucleus of the vagus (and possibly of the other) roots.

But there is yet a third source of some of the fibres of the nerves of which we are speaking. In sections through the bulb there may be seen just ventral to and a little lateral to the combined nucleus (Fig. 109, 4, 5, 6, IX. *a*), the circular section of a longitudinal bundle of fibres. In the hinder sections (Fig. 109, 4) the bundle is a very thin one and still further back it is lost to view, though there are reasons for thinking that some of the fibres are continued back into the cervical cord, as far as the origin of the fourth cervical nerve or even beyond; in the more forward sections (Fig. 109, 5 and 6), it increases in diameter and may be traced forward to the front end of the combined nucleus into which it merges. It is a bundle of fibres which, starting successively in the lateral grey matter of the cervical cord and higher up in the reticular formation of the bulb, run longitudinally forwards; the bundle at first increases in size by the addition of fresh fibres at each step; but farther forwards the fibres leave the bundle to pass into the roots of the nerves of which we are speaking, especially of the glossopharyngeal, and the bundle eventually ends in front by passing into the glossopharyngeal roots. The grey matter from which these fibres take origin does not form a defined compact area, is not therefore a nucleus in the sense in which we are now using the term, but is diffused among the rest of the grey matter along a considerable length. The fibres are nevertheless fibres of nerve roots, and the bundle is called the *ascending root* of the glossopharyngeal, the term ascending being used since it is customary to trace such structures from below upwards, that is from behind forwards; though since the fibres in question are probably afferent fibres carrying impulses backwards from the nerves to the grey matter, 'descending' would be the more appropriate word. The bundle has also been called the *fasciculus solitarius;* and, since its position has been supposed to correspond to that of the area marked out experimentally as the respiratory centre, § 361, it has been spoken of as the *respiratory bundle.*

The roots of these three nerves then, the bulbar accessory, the vagus, and the glossopharyngeal, all leaving the surface of the brain along the line between the olive and the restiform body, and all so far alike that it is impossible upon mere inspection to say where in the series the fibres of the middle nerve, the vagus, begin and end, spring from three sources, the combined nucleus, the nucleus ambiguus, and the ascending root.

§ 618. *The Eighth* or *Auditory Nerve.* This nerve differs from the other nerves which we are now considering in being a nerve of special sense; its arrangements are complicated. In a view of the base of the brain (Fig. 108, *C.*), the nerve is seen to leave the surface of the brain from the ventral surface of the fore part of the restiform body at the hind margin of the pons as two strands or roots, one of which winds round the restiform body so as to reach its dorsal surface while the other appears to sink into the substance of the bulb to the median side of the restiform body; and in a transverse section of the bulb (Fig. 110) just behind the pons the two roots may be seen embracing the restiform body, one passing on its dorsal and the other on its ventral side. The former is called the *dorsal* root (Fig. 110), or sometimes the lateral root, or since it reaches farther back or lower down than the other, the posterior or inferior root; the latter is called the *ventral* root (Fig. 111), or sometimes the median root, or since it reaches farther forward or higher up than the other, the anterior or superior root. When we come to study the ear we shall find that one division of the auditory nerve is distributed to the cochlea alone and is called the nervus cochlearis, the rest of the nerve being distributed to the utricle, saccule and semicircular canals as the nervus vestibularis. As we shall see, there are reasons for thinking that the vestibular nerve carries up to the brain from the semicircular canals impulses other than those or besides those which give rise to sensations of sound, whereas the cochlear nerve appears to be exclusively concerned in hearing; and in some structural details these two divisions of the auditory nerve differ from each other. Hence it is important to note that according to careful investigations the cochlear nerve is the continuation of the dorsal root and the vestibular nerve the continuation of the ventral root.

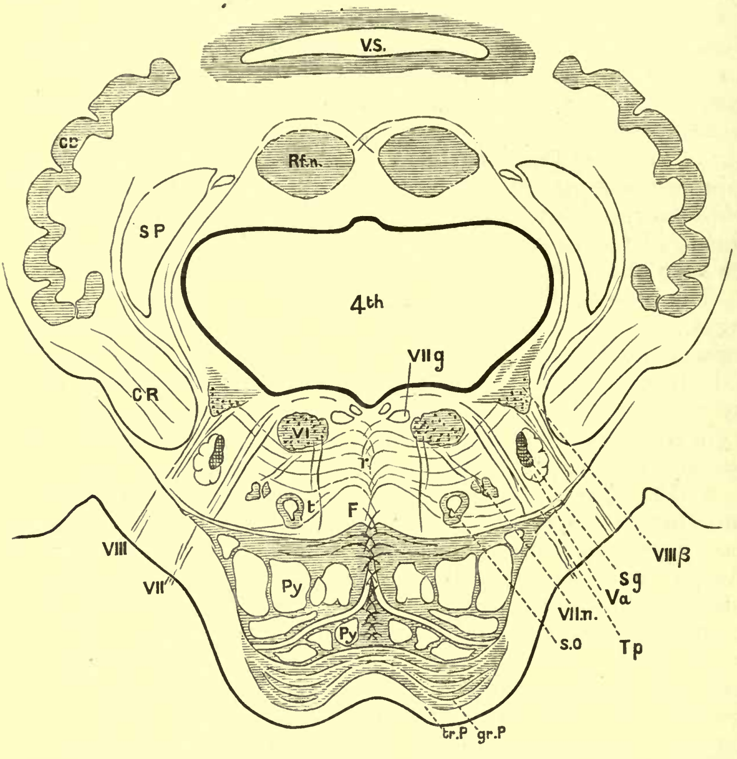

Fig. 111. Through the widest part of the Fourth Ventricle. (Sherrington.) *Taken in the line* 111. Fig. 108.

Py. Pyramidal fibres cut transversely. *tr. P.* the superficial (ventral) transverse fibres of the pons. The shaded part of the pons (*gr. P.*) indicates grey matter mingled with the deeper transverse fibres. *F.* the fillet. *Tp.* the trapezium. *C. R.* the restiform body or inferior peduncle of the cerebellum, cut across obliquely. *S. P.* the superior peduncles of the cerebellum. *r.* raphe. *s. o.* superior olive. *C. D.* corpus dentatum of the cerebellum. *Rf. n.* the nucleus of the roof. *s. g.* tubercle of Rolando. *V. S.* section through sulcus in the vermis superior of the cerebellum. *t.* bundle from the olive to the lenticular nucleus.

VIII. the eighth or auditory nerve, its ventral or vestibular root, proceeding from VIII. *β.* the front part of the lateral auditory nucleus. VII. *n.* the nucleus of the seventh or facial nerve. VI. the nucleus of the sixth nerve. VII. *g.* fibres of the seventh nerve cut across as they sweep round the nucleus of the sixth before issuing from the pons as VII.

4th. the fourth ventricle, here roofed in by the cerebellum; the shading of the central grey matter immediately surrounding the ventricle is, for the sake of simplicity, omitted.

With these roots of the auditory nerve proper also issues, a little in front of the ventral root, the small nerve called the *portio intermedia Wrisbergi*, which goes to join the facial nerve.

The auditory nucleus, as a whole, is a broad mass, having in transverse sections of the bulb a somewhat triangular form, lying in the lateral parts of the floor of the fourth ventricle, reaching in front somewhat beyond the level of the striae acusticae, and overlapping behind the front parts of the nucleus ambiguus and the combined accessory-vago-glossopharyngeal nucleus; it extends laterally some distance outside the former nucleus.

The nucleus however consists of two distinct parts, a *median* or *inner nucleus* (Fig. 115, VIII. *m.*), characterized by the presence of small cells, and a *lateral* or *outer* nucleus (Fig. 115, VIII. *l.*), the cells of which are much larger, some of them being very large. The lateral nucleus is placed somewhat deeper than, ventral to, the median nucleus; it also extends farther forwards (Figs. 110 and 111, VIII. β), so that the front end of the whole nucleus is furnished by the lateral nucleus alone which at its front end occupies a more dorsal position than at its hind end.

Moreover this auditory nucleus thus placed in the floor of the fourth ventricle is not the whole of the nucleus of the auditory nerve. At the convergence of the dorsal and ventral roots on the ventral surface of the restiform body is placed a group of cells, forming a swelling which in its general appearance and in the characters of its cells is not unlike a ganglion on the posterior root of a spinal nerve. This is called the *accessory nucleus*.

When we trace the fibres of the nerve centralwards into the brain, we find that a large number at least of the fibres of the dorsal root, cochlear nerve (Fig. 110), end, according to most observers, in the cells of the accessory nucleus, or in nerve cells lying dorsal to the accessory nucleus and especially in a group of cells giving rise to the *tuberculum acusticum*, which, small in man, is conspicuous in some animals. Hence the farther part of this dorsal root as it winds round the lateral and dorsal surface of the restiform body, consists largely, if not wholly, of fibres which are derived not directly from the trunk of the nerve, but indirectly through the relay of the accessory nucleus or of other cells. Reaching the dorsal surface of the restiform body, these fibres appear on the floor of the fourth ventricle as the *striae acusticae* (Fig. 108, *str*), and end partly in the median nucleus, partly in other regions of the bulb. The exact determination, however, of the endings of this root is a matter of considerable difficulty; some observers regard the accessory nucleus as homologous, not with the Gasserian and with the spinal ganglia, but with the other, true, cranial nuclei; and in any case we must probably consider the median division of the auditory nucleus, not as a nucleus in the sense in which we are now using it, but rather as a secondary connection within the bulb.

When we trace the ventral root, vestibular nerve (Fig. 111), inwards we find that making, according to most observers, no connections at all with the accessory nucleus, it passes (Fig. 111, viii.) to the median side of the restiform body, between it and the ascending root of the fifth nerve, and so reaches the lateral division of the nucleus, in the large cells of which most at least of its fibres are said to end and which therefore may be regarded as the nucleus of the ventral root. On this point however all authors are not agreed. The lateral auditory nucleus, with the fibres proceeding to and from it, lying as they do to the median or inner side of the restiform body proper, are sometimes spoken of as the median or inner division of the restiform body; and from the nucleus a considerable number of fibres pass up with the restiform body into the cerebellum as a continuation of this "median division of the restiform body." Some authors maintain that these fibres are continued straight on from the nerve to the cerebellum; but the more recent investigations seem to shew that they all make connections with the nerve cells of the lateral nucleus on their way. These fibres constitute a connection between the auditory (vestibular) nerve and the cerebellum, the physiological significance of which we shall see later on; we may perhaps compare it to the connection between the posterior roots of the spinal nerves and the cerebellum through (the vesicular cylinder and) the cerebellar tract.

The other central connections of the lateral nucleus are, like those of the accessory and of the median nucleus, complicated and obscure. But we may call attention to a set of fibres which, starting apparently in the accessory nucleus, run directly transverse in the ventral region of the tegmentum just dorsal to the transverse fibres of the pons, forming what is called the *trapezium* (Fig. 111, *Tp.*).

Lastly, we may add that the fibres of the peculiar *portio intermedia* appear to take origin from the accessory nucleus.

§ 619. *The Seventh* or *Facial Nerve.* The nucleus (Fig. 115, VII. and Figs. 110, 111, VII. *n.*), of this nerve (it being borne in mind that the motor fibres for the orbital region (the orbicular muscle &c.), though they run in the trunk of this nerve, really belong to the third nerve and take origin from the hind part of the nucleus of the third nerve) narrower in front than behind, reaches from the level of the striae acusticae some distance into the region of the pons, and occupies in the midst of the reticular formation, a little dorsal of the patch of grey matter called the upper olive, a position corresponding closely to that of the nucleus ambiguus. The cells of the nucleus are large, and possess well marked axis-cylinder processes, which are gathered up at the dorsal surface of the nucleus to form the root. This, rising up dorsally, describes a loop (Fig. 111, VII. *g.*) round the nucleus of the sixth or abducens nerve, running forward for some little distance dorsal to that nucleus, and then descends again ventrally, passing to the lateral side of its own nucleus, between it and the ascending root of the fifth (*Va*); it thus gains the surface of the brain at the hinder margin of the pons, lateral to

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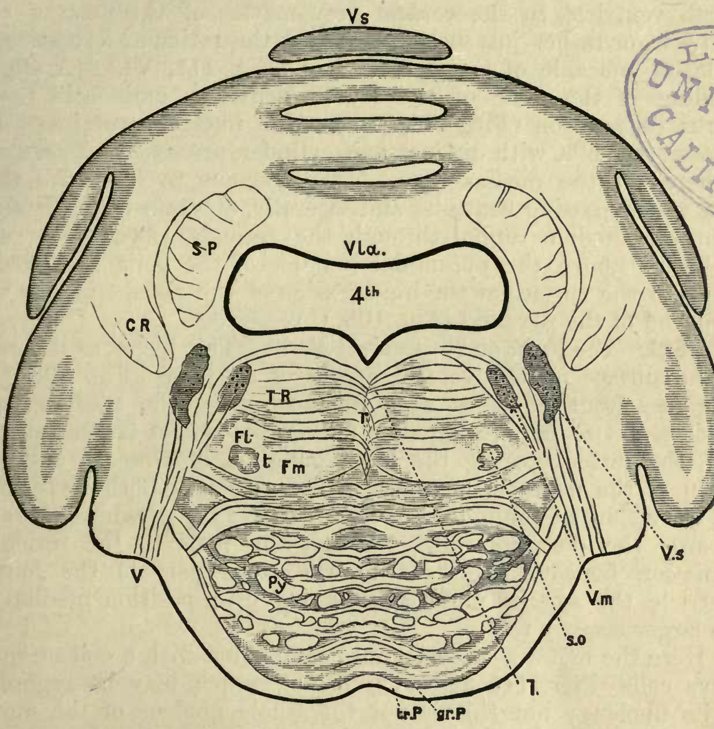

FIG. 112. THROUGH THE PONS AT THE EXIT OF THE FIFTH NERVE. (Sherrington.)

(In the line 112, Fig. 108.)

C. R. Remains of restiform body. *S. P.* superior peduncle of the cerebellum. *F. m.* median, *F. l.* lateral Fillet. *T. R.* tegmental reticular formation. *tr. P.* superficial transverse fibres of the Pons. *l.* posterior longitudinal bundles. *V. s.* superior vermix; sections of three folia are shewn, one being detached; between them the intervening sulci laid open by the section are seen. *Vl. a.* valve of Vieussens or anterior velum. *r.* raphe. *Py.* Pyramidal fibres. *gr. P.* grey matter of the Pons. *s. o.* superior olive. *t.* placed on the left side indicates the position of a bundle of longitudinal fibres which may be traced forward into the subthalamic regions. *V. m.* motor nucleus, *V. s.* sensory nucleus, and *V.* roots of the fifth nerve.

4th. fourth ventricle; shading of central grey matter omitted as in Fig. 111.

the abducens, opposite the front end of the groove between the olivary body and the restiform body. As it thus encircles the nucleus of the abducens, it looks as if it were receiving fibres from that body; but the evidence goes to shew that these fibres simply pass through the nucleus, and do not take origin from any of its cells.

§ 620. *The Sixth* or *Abducens Nerve.* This nerve starts from a compact oval nucleus (Fig. 115, VI.), lying at the level of the hinder part of the pons, and therefore of the front part of the fourth ventricle, in the central grey matter of the floor of the ventricle, or rather just between it and the reticular formation, a little on one side of the median line (Fig. 111, VI.). A slight swelling of the floor of the fourth ventricle, eminentia teres, marks its position (Fig. 115, *e. t.*). The nucleus contains fairly large nerve cells, with distinct axis-cylinder processes. These are gathered at the median side of the nucleus to form the thin root, which passing ventrally and laterally, at some little distance from the median raphe, through the reticular formation, runs backward above the pyramidal bundles of the pons, and finally comes to the surface at the hinder edge of the pons, opposite the front end of the pyramid (Fig. 108, *C.*).

§ 621. *The Fifth* or *Trigeminal Nerve.* This nerve, as it comes to the surface on the ventral aspect of the pons (Fig. 108, *C.*), near the front edge, at some distance from the median line, consists of two parts, a smaller motor root and a larger sensory root, the latter bearing the large ganglion of Gasser; and the origin of the nerve is in many ways complex. Both roots may be traced in an oblique direction (Fig. 112, V) inwards and towards the dorsal surface, through the pons to the reticular formation beneath the floor of the front part of the fourth ventricle, the smaller motor root taking up a position median to the larger sensory root.

Here the motor root comes into connection with a collection of nerve cells (Figs. 115 and 112, V. *m.*), which may be regarded as its nucleus; but this is not the whole nucleus of the motor root. From the level of the nucleus there stretches forwards as far as the level of the anterior corpora quadrigemina a bundle of longitudinal fibres which, since it is usually traced from the front backwards until it passes into the root of the nerve, is spoken of as *the descending root* of the fifth nerve.

This descending root begins as a few scattered bundles of fibres at the level of the anterior corpora quadrigemina, in the peripheral lateral part of the central grey matter surrounding the aqueduct, dorsal and lateral (Fig. 114, V. *d.*), to the nucleus of the third nerve (Fig. 114, III. *n*). From thence the fibres pass backward, augmenting in number, and soon form a compact bundle, semilunar in transverse section, lying lateral to the fourth nerve as this is rising dorsally (Fig. 113, V. *d.*); still increasing in number in their course backward they gradually assume a more ventral position as the aqueduct opens into the fourth ventricle. All along its course this descending root has attached to it large (70 μ or more in diameter), sparse spheroidal nerve cells, of striking appearance; these however seem too few to give origin to at least all the fibres, and there are some reasons for connecting this root with the collection of grey matter called ‘locus caeruleus’. Fig. 113, *l.c.*

We may probably regard this descending root as belonging to the motor division of the nerve; but it is stated that many of the fibres of this root pass into the sensory root, eventually finding their way, according to some observers, into the ophthalmic branch.

The sensory root may be similarly traced into a nucleus, the sensory nucleus (Figs. 115 and 112, V. *s.*) lying lateral to the motor nucleus, and connected with this is the striking tract of fibres, to which already we have so frequently alluded, and which is called the *ascending root* of the fifth nerve.

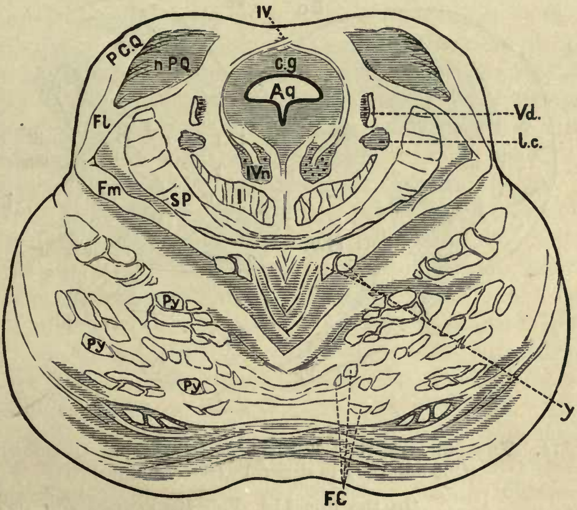

FIG. 113. THROUGH THE FORE PART OF THE PONS. (Sherrington.)

(In the line 113, Fig. 108.)

Py. Pyramidal fibres. *F. C.* Fibres from the frontal cortex. *S. P.* Superior Peduncle of the cerebellum. *F m.* median portion, *F l.* lateral portion of the Fillet. *l.* posterior longitudinal bundles. *P. C. Q.* Posterior corpora quadrigemina. *y.* Fibres which become detached from the Fillet, and further forward form (the innermost) part of the Pes of the Crus. *l. c.* locus caeruleus. *n. P. Q.* nucleus of the posterior corpora quadrigemina; the outline is made too sharp. IV. bundles of the fourth nerve decussating, IV. *n.* its nucleus. V. *d.* descending root of the fifth nerve. *Aq.* the aqueduct. *c. g.* the region of central grey matter.

This ascending root begins as a bundle or bundles of few fibres which may be traced backward as far as at least the level of the second cervical nerve, and is soon conspicuous in transverse sections (Fig. 109 *et seq.*, V. *a.*) as a semilunar patch of white matter forming a sort of cap on the outside of the swollen caput of the posterior horn, between this structure and the longitudinal fibres which are beginning to form the restiform body on the surface. Passing upwards, and continually augmenting in bulk, the root clings, as it were, to the gelatinous substance of the caput of the posterior horn, and sinks with it inwardly and ventrally as this becomes covered up first by the restiform body and subsequently by the issuing trunk of the great eighth or auditory nerve (Figs. 110, 111). Passing still forward, beyond the disappearing gelatinous substance, the root, still growing larger and divided into several distinct bundles, runs into the reticular formation of the pons and, reaching the level of the sensory nucleus, suddenly bends round and joins the sensory root.

This ascending root differs from the descending root in not having conspicuously attached to it any collection of nerve cells; in this respect it resembles the ascending root of the glossopharyngeal, and we may add part of the posterior root of an

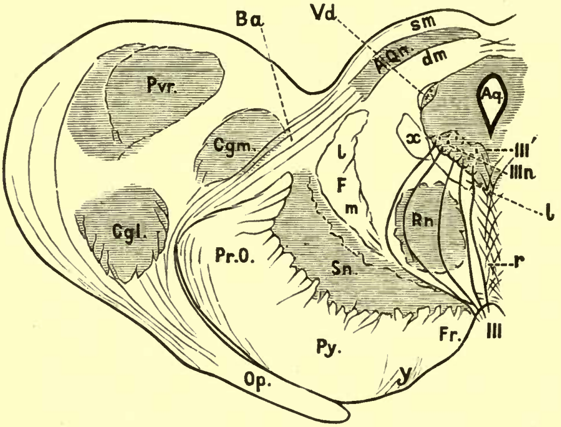

Fig. 114. Through the Crus and Anterior Corpora Quadrigemina. (One half only is shewn.) (Sherrington.)

(In the line 114, Fig. 108.)

Py. the pyramidal portion of the pes. *Fr.* the region of the pes occupied by fibres from the frontal portion of the cortex. *Pr. O.* the region occupied by fibres coming from the occipital portion of the cortex. *y.* fibres coming from the fillet. *Op.* the optic tract. *F.* the fillet, *l.* the lateral portion, *m.* the median portion. *l.* the posterior longitudinal bundle. *B. a.* the brachium of the anterior corpus quadrigeminum. *x.* fibres from the posterior commissure of the cerebrum. *r.* raphe. *S. n.* substantia nigra. *R. n.* red nucleus. *C. g. l.* lateral, and *C. g. m.* median corpus geniculatum. *Pvr.* pulvinar of optic thalamus. *A. Q. n.* nucleus or grey matter of anterior corpus quadrigeminum. III. *n.* nucleus of III. third nerve. III′. Rootlets from the dorsal part of III. *n.* the nucleus of the third nerve which cross the median line to emerge with rootlets derived from the nucleus of the opposite side. *s. m.* superficial layer of fibres of the ant. corp. quad. *d. m.* deep layer. *Aq.* aqueduct surrounded by cerebral grey matter.

ordinary spinal nerve, the fibres of which, as we have seen, pass into the grey matter without being obviously connected with nerve cells. In its lower part at least it consists of extremely fine fibres, and indeed looks very much like a continuation in the bulb of the marginal (Lissauer's) zone of the spinal cord.

§ 622. *The Fourth* or *Trochlear Nerve.* The nucleus of this nerve (Fig. 115, IV.) is a column of somewhat large multipolar cells on each side of the median line below the aqueduct (Fig. 113, IV. *n.*), reaching from the level of the junction of the anterior and posterior corpora quadrigemina to the hinder level of the latter body.

The root, starting from the lateral surface of the nucleus, does not take at first a ventral direction, but sweeps laterally and dorsally in the outer layers of the central grey matter (Fig. 113), and so curving round to the dorsal surface reaches the valve of Vieussens, where in the median line it decussates with its fellow in the substance of the valve; such a decussation at a distance from the nucleus of origin is exceptional in the cranial nerves. Leaving the surface of the brain in the valve, it takes a superficial course curving (Fig. 108, *B*) laterally and ventrally, and makes its appearance in a ventral view of the brain at the front edge of the pons, on the lateral edge of the crus (Fig. 108, *C.*).

§ 623. *The Third* or *Oculomotor Nerve.* The nucleus of this nerve (Fig. 115, III., 114, III. *n.*) is a column of, for the most part, fairly large multipolar cells lying on each side close to the median line, in the grey matter of the central canal, just dorsal to a bundle of fibres which we shall speak of as the longitudinal posterior bundle; it reaches from the level of the posterior commissure in the third ventricle to the level of the junction of the anterior and posterior corpora quadrigemina. In a section taken through its middle (Fig. 114) the nucleus is seen to give off fibres which run vertically towards the ventral surface, traversing the tegmentum and a body (*Rn.*) which we shall presently speak of as the "red nucleus," but apparently making no connections with these structures, and pierce the median edge of the pes, emerging (Fig. 108, *C.*) on the surface to the median side of each crus. As we shall see later on, this nerve is now exclusively efferent, whatever it may have been in more primitive beings. We shall also see later on, that impulses starting from the cerebrum of one side pass to the nerve of the other side, that is to say decussate; and this is also the case with the other efferent cranial nerves. The fibres which appear to take origin from the nerve cells of the nucleus do not cross over after emerging from the nucleus, but keep to the same side; there is no distant decussation as in the case just noted of the fourth nerve. There are however fibres (Fig. 114, III.') which leaving the nucleus cross the median raphe from one side to the other, and these possibly are the paths for the decussation of the

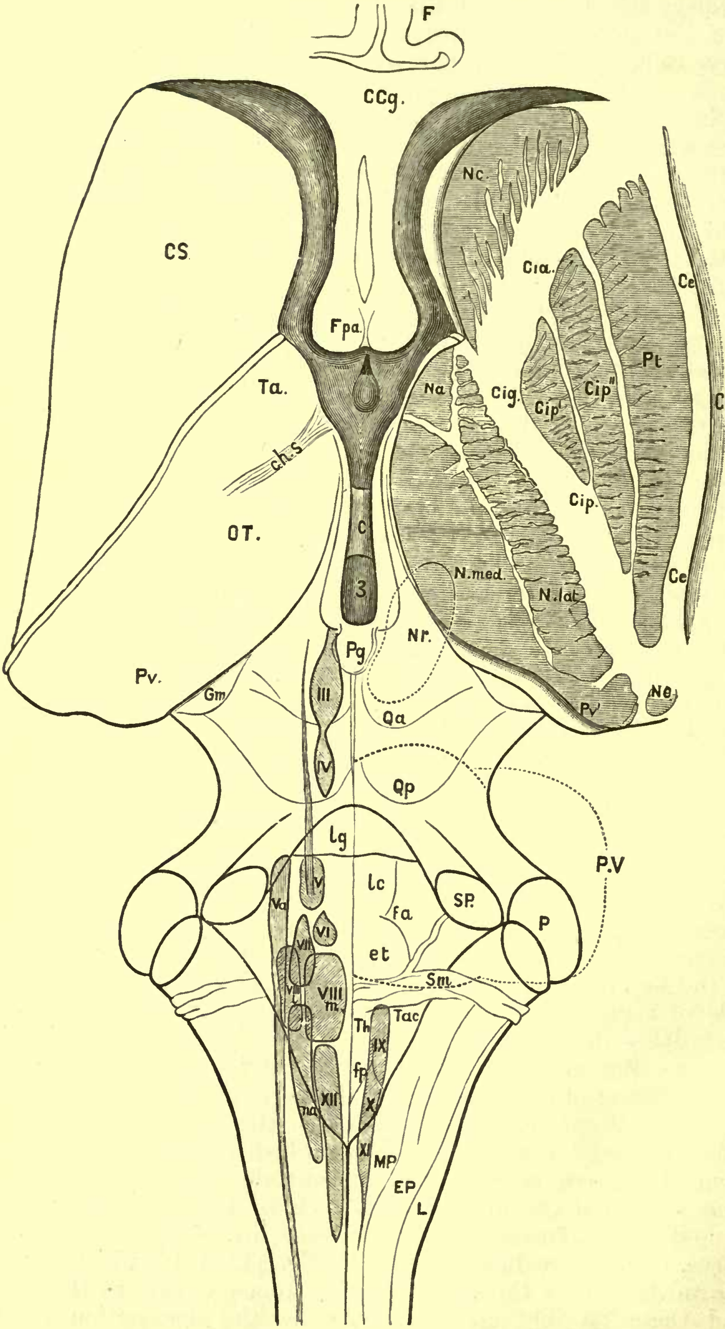
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FIG. 115. DIAGRAM TO ILLUSTRATE THE POSITION OF THE NUCLEI OF THE CRANIAL NERVES. (Sherrington.)

The brain is supposed to be viewed from the dorsal aspect, the cerebral hemispheres and cerebellum having been cut away. The nuclei are represented as if seen through transparent material. On the right side, the corpus striatum and optic thalamus have been cut away horizontally to some little depth in order to shew their internal structure.

L. lateral, *E. P.* external posterior and *M. P.* median posterior column of the cord. *I. P.* inferior peduncle, *S. P.* superior peduncle, and *P.* middle peduncle of the cerebellum, all cut across. The dotted curved lines, upper and lower, on the right half of the figure to which the dotted line *P.V.* outside the figure points, mark the upper and lower boundaries of the pons on the ventral aspect.

The outline of the fourth ventricle is shewn by a bold thick line. In the floor of the ventricle are shewn, on the right half:—*fp.* fovea posterior. *Th.* trigonum hypoglossi. *T. ac.* trigonum acusticum. *e. t.* eminentia teres. *s. m.* striae medullares or acusticae. *f. a.* fovea anterior. *l. c.* locus caeruleus. *l. g.* valve of Vieussens.

Qp. posterior and *Qa.* anterior corpus quadrigeminum. *Pg.* pineal gland. *Nr.* the outline of the red nucleus. 3, the third ventricle, in which *C* indicates the middle or soft commissure. *F. p. a.* the pillars of the fornix, behind which is indicated in the cavity of the third ventricle the hollow of the infundibulum. *C. C. g.* the genu of the corpus callosum, between which and the fornix the cavity often called the fifth ventricle is indicated. *F.* portion of convolution of frontal hemisphere cut across.

On the left side are shewn:—*C. S.* corpus striatum. *O. T.* optic thalamus. *Pv.* pulvinar. *T. a.* Tuberculum anterius. *ch. s.* choroidal sulcus marking the place of reflection of the choroidal plexus. On the right side are exposed:—*NC.* head of, *Nc*, end of tail of nucleus caudatus. *Cip′*, *Cip″* the two parts of the globus pallidus, and *Pt*, putamen of the nucleus lenticularis. *N. a.* anterior nucleus. *N. med.* median nucleus, *N. lat.* lateral nucleus and *Pv.′* pulvinar of the optic thalamus. *Cia.* front limb, *Cig.* knee or genu, *Cip.* hind limb of internal capsule. *Ce.* external capsule. *Cl.* claustrum.

The numerals III. to XII. indicate the nuclei of the respective cranial nerves, all shewn on the left side with the exception of the accessory-vago-glosso-pharyngeal IX. X. XI., which to avoid confusion is placed on the right side. *V.* is the motor nucleus of the fifth nerve with the descending root, *V. a* the sensory nucleus of the same with the long ascending root. VIII. *m.* median nucleus, VIII. *l.* lateral nucleus of the auditory nerve. *n. a.* nucleus ambiguus. The ascending root of the ninth nerve is seen at the hind end of the combined nucleus of IX. X. XI.

impulses; but they may be fibres passing from the crus across the raphe to the nucleus. This nerve has special relations with the optic tract, but of these we shall speak when we come to deal with the functions of the nerves.

§ 624. In attempting to understand the nature and relations of these cranial nerves, it must be borne in mind that, while morphological studies lead us to believe that, as the vertebrate body has been developed out of an invertebrate ancestry, so the brain of the vertebrate has arisen by a series of modifications from the nervous structures placed at the head and around the mouth of an invertebrate, the same studies teach us that such an evolution has been accomplished by means of profound changes. We have, for instance, reason to think that the mouth of the vertebrate does not correspond to the mouth of the invertebrate, but is a new structure, whose appearance has been accompanied by a considerable dislocation of parts. We must accordingly expect to find the indications of a segmental arrangement greatly obscured on the one hand by transposition, and on the other by fusion.

The twelfth or hypoglossal nerve is one whose nature seems fairly simple. It is in function exclusively an efferent nerve. The large cells, with conspicuous axis-cylinder processes, which characterize its nucleus, are exactly like those of the anterior horn of the spinal cord which give origin to the fibres of an anterior root. The nucleus moreover in its position corresponds to part of the anterior horn of the spinal cord, if we take into account the shifting involved in the decussation of the pyramids, and in the new developments of the bulb. If we compare Fig. 109 with any section of the cord, we see that the hypoglossal nerve corresponds to an anterior root of the spinal cord, but that the fibres, after leaving the cells from which they take origin, traverse in the former a large tract, and in the latter case a small tract of tissue. Whether the whole nerve corresponds to the fibres of several segments fused together, or to those of one segment spread out longitudinally, is for our present purposes of secondary importance.

Recognizing the hypoglossal nerve as the homologue of a spinal anterior root, we may go on to claim the nuclei of the third and fourth nerves as similar groups of cells of the anterior horn, giving rise to anterior roots. The position of the nuclei, the character of the cells, the function of the fibres, all support this view. The case is perhaps not so clear as that of the hypoglossal nerve, since there are reasons for thinking that these nerves have undergone in the course of evolution greater changes than has the hypoglossal nerve; still these reasons do not oppose the above conclusion.

The nucleus of the exclusively motor sixth nerve does not exactly correspond to those of the third and fourth in position; but we may probably place it in the same series with them. Thus we have in succession, the third, fourth, sixth, and twelfth nerves, with their respective nuclei, as the anterior roots of nerves of their several segments.

In the fifth nerve, the dislocation and fusion spoken of above has introduced difficulties. The motor nucleus, with the fibres of the motor root to which it gives origin, has by some been considered as homologous to the series just described; but it is at once obvious that we cannot look upon this great fifth nerve as corresponding to one spinal nerve, with its anterior and posterior root, great as the superficial resemblance seems to be. The features of the remarkable ascending root forbid this. The fibres of this root may be traced back, as we have said, to the very beginning of the bulb, and indeed into the spinal cord beyond; as far as can be ascertained, they are not in an obvious and direct manner connected with nerve cells along their course; but the bundle of fibres clings, as we have seen, to the gelatinous substance of the posterior horn of the spinal cord and to the continuation of this along the bulb, and the fibres are lost in this structure. The root, therefore, as we have said, corresponds very closely to part at least of the posterior root of a spinal nerve, and, though the matter has not yet been experimentally proved, we may infer that the trophic centres of these fibres are to be found in the cells of the Gasserian ganglion.

But if this ascending root be of the nature of a posterior root (and we may incidentally remark that the term ascending has been unhappily chosen, since, if it be an afferent root, the direction of the impulses which it carries will be a descending one, namely from the entrance in the pons towards the hinder parts), we can hardly suppose that it belongs to a single segment, or is the complement of the motor root alone; in it, most probably, the posterior fibres of several segments are blended together. Further, we may perhaps infer that the other fibres of the sensory root which end directly in what we have called the sensory nucleus, are in nature quite distinct from the fibres of the ascending root; and if so, difficulties arise as to the nature and homologies of the nucleus in question. These, however, we must not discuss here, nor can we enter into the question of the nature of the descending root, concerning the fibres of which, as we have said, authorities differ as to whether they pass into the motor or sensory root. We have said enough to shew that this fifth nerve is extremely complex, and that its apparent conformity to a simple spinal nerve is in reality misleading.

The fibres of the vagus, glossopharyngeal, and bulbar accessory, taken together, are partly efferent, partly afferent. The combined nucleus of these three nerves, the cells of which are small and devoid of conspicuous axis-cylinder processes, is usually regarded as a sensory nucleus, and in the diagram, Fig. 115, is shaded accordingly. It may perhaps be compared to the sensory nucleus of the fifth. Thus, the ascending root, or fasciculus solitarius, presents many analogies with the ascending root of the fifth, and we are led to regard this as, like it, a gathering of certain afferent fibres of the posterior roots of several segments; in its case also the term ascending is misleading. But there are many difficulties in connection with this nucleus, as with the fifth. We must not enter into a detailed discussion concerning them, but may remark that we have here perhaps to deal with complexities due to the fact that certainly many vagus and glossopharyngeal fibres, and probably some of those of the fifth, are splanchnic in function.

The nucleus ambiguus contains large conspicuous cells and we may probably regard it as a motor nucleus, especially of the vagus fibres. We may also perhaps place it and the nucleus of the seventh nerve in the same category, and further class with them the motor nucleus of the fifth, looking upon all three as so many detached portions of grey matter, corresponding to some part of the anterior horn of the spinal cord. Whether they are exactly homologous to the hypoglossal nucleus, and their fibres to simple anterior roots, is not so clear.

Lastly, the auditory nerve, both from its character as a nerve of special sense and from the remarkable features of its nuclei, is even more difficult. Most probably it results from the fusion of more roots than one; but it is impossible at present to obtain a clear conception of the nature of the whole nerve.

2. *The Superficial Grey Matter.*

§ **625.** The whole of the surface of each cerebral hemisphere for some little depth inwards consists of grey matter, possessing special characters; this is called the cortical grey matter, or the *cortex cerebri,* or shortly and simply the *cortex.* As we shall see, by its histological and still more by its physiological features, it stands apart from all other kinds of grey matter.

The whole of the surface of the cerebellum is also covered with grey matter, which, while possessing features of its own, so far resembles the cerebral cortex in its histological characters that it too has been spoken of as cortex, as the cortex cerebelli. By its functional manifestations, however, it differs widely from the cerebral cortex; and since there are many advantages in being able to use the word cortex in connection with the cerebrum only, it is desirable not to speak of a cerebellar cortex but to employ the term "superficial grey matter of the cerebellum."

The third ventricle and the hinder part of the fourth ventricle are not roofed in by nervous material, and possess no superficial grey matter at all. In the corpora quadrigemina, which form the roof of the aqueduct or cavity of the mid-brain, grey matter is present and possesses, in the case of the anterior corpora quadrigemina at least, characters to a certain extent analogous to those of the cortex and to the cerebellar superficial grey matter; but it will be best to consider the grey matter of these bodies as belonging to another category.

3. *The Intermediate Grey Matter of the Crural System.*

§ **626.** We have seen (§ 603) that the crura cerebri form the prominent part of a system of longitudinal fibres stretching from each cerebral hemisphere to the bulb and to the spinal cord. This system of fibres, upon which we may consider the various parts of the brain to be as it were founded, we may speak of as the crural system. It is, it is true, not one continuous strand, but a number of different strands, having different beginnings and endings; but these all contribute to the crura and are so far alike as to justify us in considering them as a system. The cortical grey matter of each hemisphere is, as we shall see, connected with various parts of this system, and in one sense we may regard this system as beginning in the cortex of each hemisphere, and ending in the spinal cord. But certain masses of grey matter in the hemisphere not strictly cortical, and several important masses and areas of grey matter lying between the hemisphere and the cord, are connected with the system; and these we may speak of as the "intermediate grey matter of the crural system."

Corpus striatum and *optic thalamus.* Of all these several collections of grey matter, the largest, most conspicuous, and perhaps the most important are the two masses in the front part of the system known as the corpus striatum and optic thalamus. The former is, as we have seen (§ 602), a development of the wall of the cerebral vesicle, the latter a development of the wall of the vesicle of the third ventricle. They are therefore of different origin; although in the course of the growth of the brain they become closely attached to each other, they are at the outset quite separate and distinct. Moreover, as we shall see, they differ from each other so essentially, in their nature and relations, that they cannot be considered as homologous bodies; and the term "basal ganglia" often applied to them is therefore unfortunate. Nevertheless it will render the description of their topographical relations easier, if for a little while we consider them together.

When the lateral ventricle is laid open from above, part of the corpus striatum is seen projecting into the cavity of the ventricle. In front the projecting part is broad, forming the lateral wall and part of the floor of the ventricle, and to its median side lies the cavity of the ventricle, separated from its fellow by the septum lucidum. Farther back the projecting part, becoming gradually narrower, assumes a more lateral position and passes into the descending horn. In this part of its course there lies on its median side, separated from it by a narrow band called the tænia semicircularis or stria terminalis, the optic thalamus, a narrow strip of the surface of which is seen projecting outside the edge of the choroid plexus. If now, not only both lateral ventricles be laid open by removal of the corpus callosum and the fornix with the velum interpositum and choroid plexus be taken away, so as fully to expose the third ventricle, but also, in order to obtain a better view, the whole of the hinder part of the cerebrum containing the posterior horns of the lateral ventricle, be completely cut away, it is seen (Fig. 115) that the two optic thalami (*O. T.*) present themselves as two large oval bodies, placed obliquely athwart the diverging crura cerebri and converging in front to form the immediate walls of the third ventricle. In front and to the sides of the optic thalami are seen the corpora striata (*C. S.*) forming anteriorly the lateral walls of the two lateral ventricles, and diverging behind to allow of the interposition of the optic thalami. On each side of the brain then these two bodies, the corpus striatum and optic thalamus, appear as two masses of grey matter placed on the crus cerebri as this, diverging from its fellow, begins to spread out into the cerebral hemisphere, the corpus striatum being placed somewhat in front of the optic thalamus. The relations of the two bodies moreover are such that while the optic thalamus alone forms the wall of the third ventricle to which it properly belongs, and the corpus striatum forms part of the wall of the lateral ventricle to which it in turn properly belongs, the optic thalamus also projects into and seems to form part of the wall of the lateral ventricle, though at its origin it had nothing to do with the cerebral vesicle.

We spoke just now of these bodies as being placed on the crura cerebri, but though their dorsal surfaces thus project from the dorsal surface of the diverging crura, a large portion of each body is, so to speak, imbedded in the substance of the diverging crus, and what is seen in the above surface view is only a part of each body, and indeed, in the case of the corpus striatum, only a small part. In order to understand the nature and relations of these two important bodies we must study sections taken through a cerebral hemisphere in various planes (Figs. 116—123).

Each crus is made up as we have seen of a dorsal portion or tegmentum consisting largely of grey matter, and a ventral portion or pes consisting exclusively of longitudinally disposed fibres. The tegmentum ends partly in structures lying ventral to the thalamus, partly in the thalamus itself; and we may for the present leave this part of the crus out of consideration. The fibres of the pes, while continuing their oblique course forwards and outwards, soon rise dorsally by the side of the thalamus and hence, in a transverse dorso-ventral section at the level of the hind part of the thalamus (Fig. 116), are seen leaving their previous position ventral to the substantia nigra (*Sn*) and passing (*Cip*) by the side of the thalamus on their way to the central white matter of the hemisphere. In this part of their course they form a thick strand separating the thalamus (*ln*) from a large mass of grey matter which, roughly triangular in section, is divided by partitions of white matter into three parts (*Gp′*, *Gp″*, *Pt*), and of which we shall speak directly as the nucleus lenticularis.

If instead of taking a transverse we take a longitudinal dorso-ventral (or as it is called sagittal) section (Fig. 122) we find that the fibres forming the strand in question do not continue parallel to each other as they rise dorsally but diverge in a radiating manner, forming the so-called corona radiata. If again we take horizontal sections at proper levels (Figs. 115, 121), we find that this strand or rather thick band of dorsally directed radiating

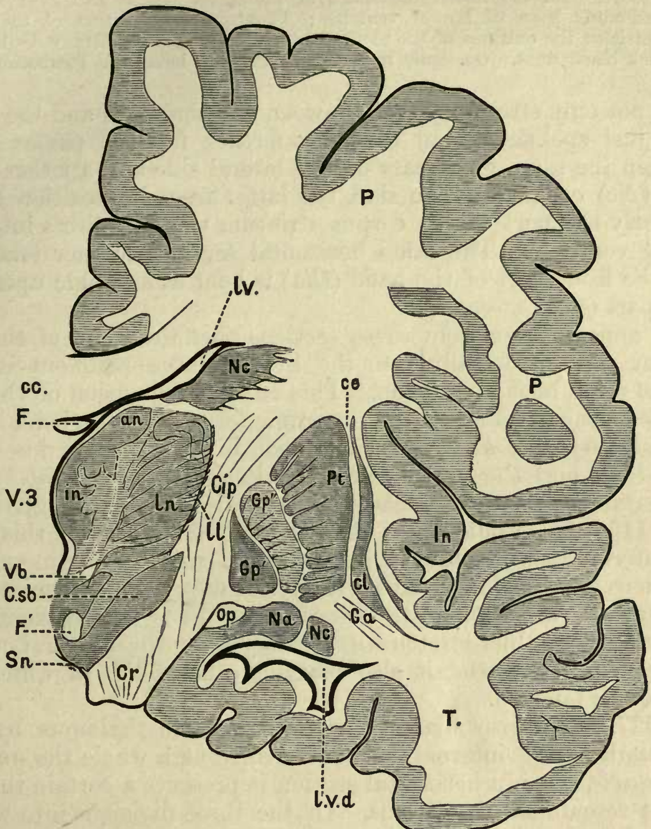

Fig. 116. Diagrammatic outline of a transverse dorsoventral section through the Right Hemisphere (Man), at level posterior to the knee of the internal capsule. (Natural size.) (Sherrington.)

Nc, nucleus caudatus; in the upper part of the figure, the section of the nucleus is through the narrower portion which succeeds the wider front end or head; in the lower part of the figure the section passes through the tail of the nucleus near its end, and this portion of it has for the sake of clearness been sundered from the grey matter of *Na*, nucleus amygdalæ, more distinctly than in reality is the case. *Gp'*, *Gp''* globus pallidus, seen here in two segments, and *Pt.* putamen of nucleus lenticularis. *an.* the anterior, *in.* the inner, and *ln.* the lateral nucleus of the optic thalamus; at *ll.* is seen the "latticed layer" lying next to *Cip.* the posterior limb of the internal capsule and containing many strands of fibres which mingle with it. In the thalamus between the anterior and internal nuclei on the one hand and the lateral nucleus on the other is a layer shaded less deeply in the figure, representing the internal medullary lamina of the thalamus, consisting largely of white matter. Other collections of white matter within the thalamus are *Vb*, the bundle of Vicq. d'Azyr and *F'* the lower end of the anterior pillar of the fornix. *F.* The upper end of the anterior pillar of the fornix, below *cc* the corpus callosum. *Csb.* corpus subthalamicum, forming a fairly continuous mass with the thalamus; *Sn.* substantia nigra. *cl.* Claustrum; *ce.* external capsule. *Ca.* terminal portion of anterior commissure. *In.* the insula or island of Reil. *lv.* lateral ventricle; *l. v. d.* descending horn of lateral ventricle; *V.* 3. in the position of the third ventricle; the outlines of the cavities are made diagrammatically distinct by thick black lines. *Op.* optic tract; *P, P.* Parietal lobe. *T.* Temporal lobe.

fibres not only stretches (*Cip*) between the thalamus and the grey mass just spoken of, but reaching farther forward passes (*Cia*) between the same grey mass on the lateral side and another grey mass (*Nc*) on the median side, the latter from its position being evidently the part of the corpus striatum which projects into the lateral ventricle. The same horizontal sections further teach us that the front part of the band (*Cia*) is bent at an angle upon the hind part (*Cip*).

It appears then from these sections that the fibres of the pes as they rise up dorsally into the hemisphere spread out in the form of a fan bent upon itself. This fan-like expansion of the pes is called the *internal capsule*, the angle formed by the bend being called its *genu* or *knee*, (*Cig*) the part in front of the knee the *front limb*, and the part behind the knee the *hind limb*. And horizontal sections at levels more dorsal than those given in Figs. 115—121 would shew that the fibres composing this fan-like internal capsule, as they rose dorsally, curved away in various directions to reach nearly all parts of the surface of the hemisphere. We may add that though the internal capsule is mainly composed of fibres which thus stretch all the way from the cerebral cortex to the pes of the crus, it also contains other fibres of which we shall speak later on.

§ **627**. The grey mass separated from the thalamus by the hind limb of the internal capsule is called as a whole the *nucleus lenticularis*, since in horizontal section it presents a certain though distant resemblance to a lens. Of the three divisions into which it is split up by the partitions of white matter, the two median ones *Gp′*, *Gp″* are spoken of together as the *globus pallidus*, the name being given to them on account of their paler colour. The third, lateral division *Pt*, is called the *putamen*. The use of these two names for the two different parts of the one body, appears to be justified by the different connections and features of the two parts.

The grey mass which in a horizontal section (Fig. 115, *Nc*) is separated from the nucleus lenticularis by the front limb of the external capsule, and which projects into the lateral ventricle, is called the *nucleus caudatus*. The nucleus caudatus and the nucleus lenticularis form together the corpus striatum; the former, since it projects into the lateral ventricle, being the part of the corpus striatum seen when the lateral ventricle is laid open, is sometimes spoken of as the intraventricular portion of the whole body, while the nucleus lenticularis, which is wholly hidden in the hemisphere and in no part projects into the lateral ventricle, is called the extraventricular portion.

But only a part, indeed only a relatively small part, of the nucleus caudatus is disclosed in such a horizontal section; to learn the somewhat peculiar form and relations of the whole nucleus a

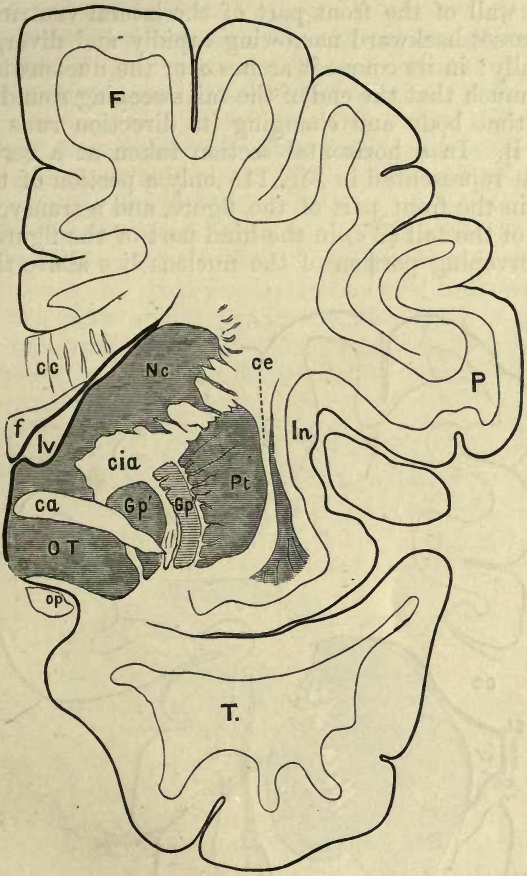

FIG. 117. DIAGRAMMATIC OUTLINE OF A TRANSVERSE DORSOVENTRAL SECTION THROUGH THE RIGHT HEMISPHERE (MAN) AT A LEVEL ANTERIOR TO FIG. 116. (Natural size.) (Sherrington.)

Nc. nucleus caudatus; *Gp'*, *Gp''*, globus pallidus, seen here in two segments, and *Pt.* putamen of nucleus lenticularis; *OT.* optic thalamus with *ca.* anterior commissure in close relation to *cia*, anterior limb of internal capsule. *ce.* external capsule. *op.* optic tract. *cc.* corpus callosum, *f.* fornix. *lv.* a space that in its upper part belongs to the lateral ventricle, in its lower was filled by the fold of subarachnoid tissue and pia mater the side fringe of which, covered with epithelium, forms the choroid plexus; this fold was detached in the making of the section and was removed. *In.* the insula; *F.* Frontal lobe; *P.* Parietal lobe; *T.* Temporal lobe.

For greater clearness, the cortical grey matter, which is shaded in Fig. 116, is in this figure left unshaded.

number of sections of a hemisphere taken in different planes must be studied; and these will at the same time explain why the nucleus is called 'caudatus.' These teach us that the nucleus has somewhat the form of a comma (Fig. 119). The thick rounded head forms the lateral wall of the front part of the lateral ventricle; thence the body passes backward narrowing rapidly and diverging somewhat laterally; in its course it arches over the nucleus lenticularis, curving so much that the end of the tail sweeping round the hinder border of that body and changing its direction runs eventually ventral to it. In a horizontal section taken at a certain depth such as that represented in Fig. 115 only a portion of the head or body (*Nc*) in the front part of the figure, and a transverse section of the end of the tail (*Nc*) in the hind part of the figure are seen; all the intervening portion of the nucleus lies above the plane of

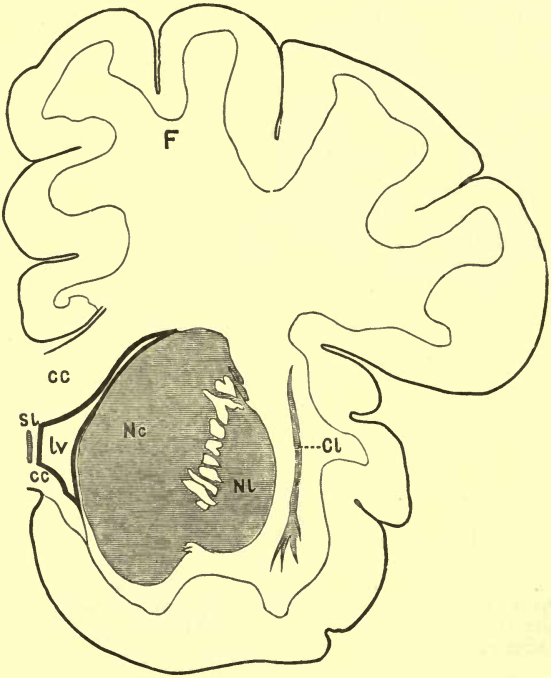

Fig. 118. Diagrammatic outline of a transverse dorsoventral section of Right Hemisphere (Man) through the frontal lobe. (Natural size.) (Sherrington.)

Nc. Head of nucleus caudatus, and *Nl.* the front end of the putamen of the nucleus lenticularis becoming fused with it. *c. c.* corpus callosum, cut through at its front bend or rostrum so that both dorsal and ventral portions are shewn; between these is seen the fifth ventricle or cavity in the septum lucidum *Sl.* *lv.* lateral ventricle. *Cl.* claustrum. *F.* Frontal lobe.

Cortical grey matter, as in Fig. 117, left unshaded.

the section. In a transverse, dorso-ventral, section taken somewhat anteriorly through the front limb of the capsule, Fig. 117, the head or body of the nucleus caudatus (*Nc*), which has not yet reached its greatest dimensions, is seen lying dorsal to the nucleus lenticularis, separated from it by the white mass of the front limb (*cia*) of the capsule, though this is somewhat broken up by strands of grey matter passing from one nucleus to the other. In a transverse, dorso-ventral section, taken still more anteriorly, through the frontal lobe (Fig. 118), the head of the nucleus caudatus is seen at about its greatest size, and the diminishing nucleus lenticularis (*Nl*), represented by the putamen alone, is becoming fused with it, the two nuclei being separated by a small quantity of white matter of the internal capsule and that largely broken up by bridles of grey matter, giving rise to a striated appearance. In a similar section still farther forward, the nucleus lenticularis would be absent, the head of the nucleus caudatus appearing by itself. Returning to the hinder part of the hemisphere, we find in a dorso-ventral section taken through

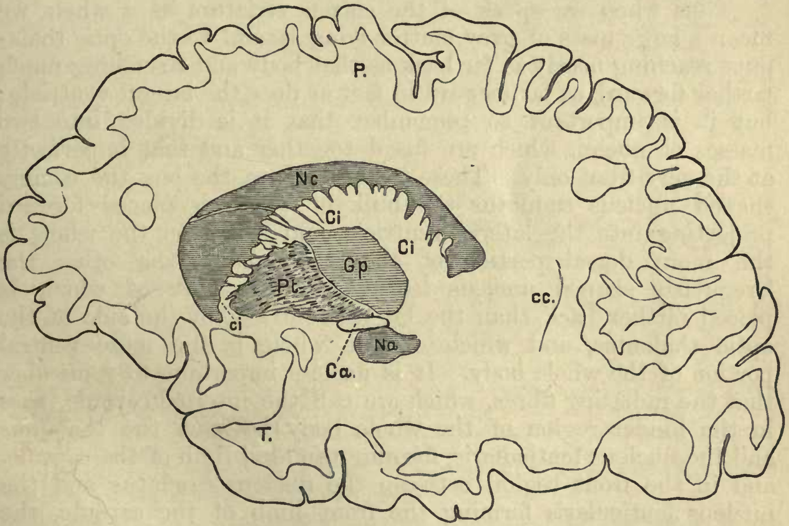

FIG. 119. DIAGRAMMATIC OUTLINE OF A SAGITTAL SECTION TAKEN THROUGH THE RIGHT HEMISPHERE (MAN) SEEN FROM THE MESIAL SURFACE. (Half Natural size.) (Sherrington.)

The plane of the section is not truly sagittal, but slightly inclined.

Nc, the caudate nucleus exposed, to the left of the letters *Nc* in nearly its entire anterior extent, to right of the letters in a considerable part of its posterior extent. It forms an arch of grey matter over the grey matter of *Pt* the putamen and *Gp* the globus pallidus of the lenticular nucleus. *Na*, the amygdaloid nucleus. *Ci*, *Ci*, *Ci*, the internal capsule; *Ca*, the anterior commissure; *cc*, the hinder limit of fibres of the splenium corporis callosi. *P*. the parietal lobe; *T*. the temporal.

the hind limb of the capsule, Fig. 116, that while the nucleus lenticularis is here at its greatest size, the head of the nucleus caudatus (*Nc*), lying dorsal to the nucleus lenticularis and separated from it by a considerable thickness of internal capsule, has much diminished; the same section moreover shews, ventral to the nucleus lenticularis and clinging to the descending horn of the lateral ventricle (*l.v.d.*), the extreme tip of the tail of the nucleus caudatus (*Nc*) soon about to fuse with the small mass of grey matter called the *nucleus amygdalae* (*Na*). A sagittal (longitudinal dorso-ventral) section taken at some distance from the median line (Fig. 119), shews the curved course of the larger portion of the nucleus caudatus, the extreme head as well as the latter part of the tail lying out of the plane of the section; and a similar section taken nearer the middle line (Fig. 122) shews how the nucleus in the middle portion is broken up by bands of fibres of the internal capsule traversing it, and thus contributing to the striated appearance; the same section also shews that the globus pallidus as well as the putamen becomes continuous with the nucleus caudatus.

Thus when we speak of the corpus striatum as a whole we mean a large mass of grey matter lying lateral to the optic thalamus, reaching nearly as far back as that body and stretching much farther forward, as far forward in fact as does the lateral ventricle; but it is important to remember that it is divided into two masses or nuclei, which are fused together and that imperfectly at the very front only. These two nuclei are, the one the comma shaped nucleus caudatus the bulk of which is placed forward projecting into the lateral ventricle, and which on the whole is the more dorsal portion of the whole body, the other the irregularly shaped nucleus lenticularis the bulk of which is placed farther back than the lateral ventricle, by the side of the optic thalamus, and which on the whole is the more ventral portion of the whole body. It is no less important to remember that the radiating fibres, which we call the internal capsule, pass in the hinder region of the whole body between the thalamus and the nucleus lenticularis, forming the hind limb of the capsule, and in the front region between the nucleus caudatus and the nucleus lenticularis forming the front limb of the capsule, the front and hind limbs being bent on each other so as to form an angle, the so-called knee.

§ **628.** The optic thalamus as a whole is a somewhat oval mass of grey matter, lying as we have said athwart the diverging crus, in which it is partly imbedded. Its curved median side covered with a thin layer of central grey matter forms the lateral wall of the third ventricle (Figs. 115, 116, 121), and in a longitudinal vertical section of the brain taken in the line of the middle of the third ventricle (Fig. 120, O.T.) is seen occupying the space between the fornix and hind end (splenium) of the corpus callosum

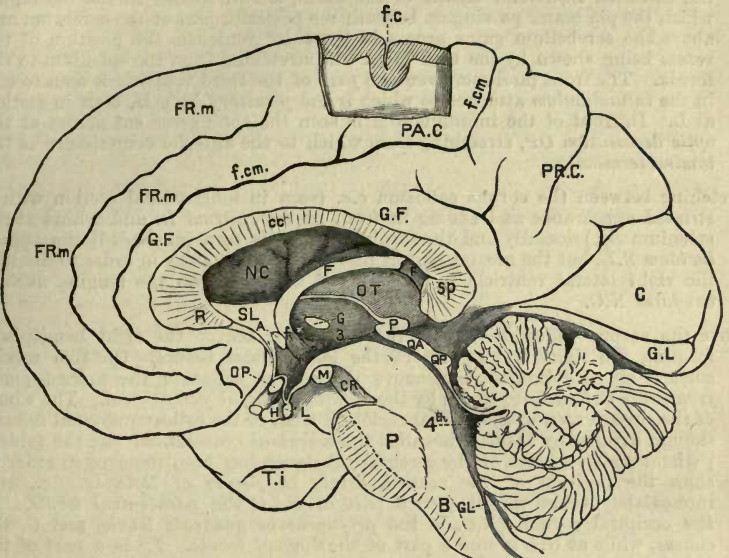

FIG. 120. VIEW OF RIGHT HALF OF BRAIN OF MAN, AS DISCLOSED BY A LONGITUDINAL SECTION IN THE MEDIAN LINE THROUGH THE LONGITUDINAL FISSURE. (Half natural size.) (Sherrington.)

The *bulb*, seen in longitudinal section at *B*, passes into the *pons P*, and into the *crus cerebri*, which last is cut obliquely across as it diverges into the hemisphere and passes out of the section. A part of the ventral surface of the crus is shewn in the shaded part marked *C.R.* At *GL* the *central canal* of the spinal cord is seen opening out into the *fourth ventricle* (4th) overhung by the cerebellum (bisected in the middle line), and passing on by the *aqueduct* beneath the *posterior*, *Q.P*, and *anterior*, *Q.A*, *corpora quadrigemina* into the *third ventricle* (3). The posterior corpus quadrigeminum is continuous behind with the *valve of Vieussens*, attached to the superior peduncle of the cerebellum, and seen in a longitudinal section overhanging the front part of the fourth ventricle. The corpora quadrigemina appear relatively small because the section passes in the median line in the depression between the right and left bodies of the two pairs; and immediately in front of them is the section of the mesially placed *pineal gland P.* which overhangs the opening of the aqueduct into the third ventricle, and the right arm of which running in the lateral wall of the third ventricle is shewn by an unshaded tract.

The roof of the third ventricle is seen to be furnished by the arch of the *fornix F*, shewn unshaded in longitudinal section. Posteriorly the body of the fornix passes into the diverging right *posterior pillar*, where *F* is shaded, and is lost to view under the overhanging rounded hind end or *splenium Sp.* of the *corpus callosum.* In front the body of the fornix is seen passing just behind the transverse section of the *anterior commissure A*, into the diverging right *anterior pillar*, *f*, which is lost to view as it stretches in the lateral wall of the ventricle towards the *corpus mammillare* or *albicans M.* The small white cross immediately behind *f*, indicates the position of the *foramen* of *Monro*. The bulging median surface of the *optic thalamus*, *O.T*, is seen forming the lateral wall of the hinder (and, owing to the cranial flexure, the more dorsal) part of the third ventricle, and on this below the area of the pineal gland is seen, unshaded, the section of the *soft* or *middle commissure C.* Between the pineal gland (*P*) and the splenium *Sp*, is seen the hind end or *pulvinar* of the thalamus projecting into the so-called transverse fissure of the brain, shewn shaded in the figure, by which the pia mater passing on beneath the posterior part of the cerebrum and above the cerebellum gains access to the third ventricle, the position of the *velum* being shewn by the thin black line stretching from the splenium to the fornix. The front (and more ventral) part of the third ventricle is seen to end in the *infundibulum* attached to which is the *pituitary body H*, seen in section at *L*. In front of the infundibulum is seen the *optic nerve* cut across at the *optic decussation OP*, stretching from which to the anterior commissure is the *lamina terminalis*.

Stretching between the corpus callosum *c.c.* (seen in longitudinal section with a striated appearance and ending in front at the *rostrum R.* and behind at the splenium *Sp.*) dorsally and the fornix ventrally is seen (unshaded) the *septum lucidum S.L*, but the greater part of this has been cut away in order to disclose the right lateral ventricle in the wall of which is seen the bulging *nucleus caudatus N.C.*

Above the corpus callosum is seen the mesial surface of the right hemisphere forming the right lateral wall of the longitudinal fissure. On this mesial surface appears immediately above the corpus callosum the arched *gyrus fornicatus G.F*, defined above by the *calloso-marginal fissure f.cm.* The whole of the surface seen in the frontal region in front of the calloso-marginal fissure, though divided by fissures, is called the *marginal convolution.* In the middle parietal region a block of the cerebral substance has been removed in order to shew the position of the *central fissure* or *fissure of Rolando*, *f.c.*, and immediately below this is seen a part of *PA.C* the *paracentral lobule.* In the occipital region *PR.C.* is the *precuneus* or *quadrate lobule*, and *C*, the *cuneus*, while at *G.L* is seen a part of the *lingual lobule. T.i* is a part of the *inferior temporo-occipital convolution*, the greater part of which is hidden to view by the pons and crus.

above, and the diverging crus below. Its more or less straight lateral border abuts on the internal capsule (Figs. 115, 116, 121). Its dorsal surface, as we have already seen, also forms part of the wall of the third ventricle and is free; but there lies close above it the prolongation of the pia mater, forming the velum interpositum with its choroid plexus (§ 602), which creeps in over it beneath the projecting hind end of the corpus callosum and the fornix (Fig. 120). Its ventral surface is fused with the crus; indeed the tegmental or dorsal portion of the crus may be said to end in it and in certain structures lying ventral to the thalamus, in what is called the "subthalamic region" (Fig. 116), while the fibres of the pes pass first ventral and then lateral to it to form the internal capsule.

The grey matter of the whole body is more or less distinctly divided by sheets of white matter, as seen both in horizontal and in vertical sections (Figs. 115, 116, 121), into three parts which have received the name of nuclei, namely the *median* or *inner nucleus* (Fig. 116, *in*) which with the thin layer of central grey matter forms the side wall of the third ventricle, the larger *lateral nucleus* (*ln*) which abuts upon the internal capsule, and the small *anterior nucleus* (*an*) which lies on the dorsal surface of the front part of the body and which thus at its front end appears to project into the lateral ventricle.

These three nuclei form however not the whole of the optic thalamus, but only the larger front portion; behind them lies the important portion called the *pulvinar*, into which the hind part of the median nucleus merges; this is partly imbedded in the crus ventrally and in the hemisphere laterally, and is partly free, coming to the surface beneath the hind end of the corpus callosum. In a median longitudinal section of the brain (Fig. 120), it is the pulvinar which forms the cushion-like (hence the name) end of the thalamus beneath the overhanging splenium of the corpus callosum, by the side of the pineal gland; and in the horizontal view (Fig. 115, *Pvr*), in which the hemispheres are supposed to have been removed, the same pulvinar is seen projecting over the crus by the side of the anterior corpus quadrigeminum. The buried portion of the pulvinar is exposed in a transverse section taken through the anterior corpus quadrigeminum, Fig. 114; the extreme end of this part of the pulvinar (*Pvr*) is here seen lying dorsal and lateral to the pes of the crus, immediately above two masses of grey matter, the corpora geniculata (*Cgl. Cgm.*), of which we shall speak later on. One of these, the *lateral* corpus geniculatum (*C.g.l.*), is especially connected with the optic tract (*op*), and, as we shall see hereafter, the pulvinar itself is also connected with the optic tract and is an important part of the central apparatus of vision.

§ **629**. The *substantia nigra, the red nucleus and other grey matter of the tegmentum.* Nerve-cells and groups of nerve-cells, or areas of grey matter, too small to deserve special names, are scattered throughout the tegmentum along its course. But, besides these and the nuclei of the third and fourth cranial nerves, of which we have already spoken, certain larger collections of grey matter deserve attention. A conspicuous mass of grey matter, circular in transverse section, placed in the midst of the tegmentum on each side but somewhat near the middle line, and stretching from the hinder margin of the third ventricle beneath the anterior corpus quadrigeminum (Figs. 114, 115), is, from the red tint it possesses, called the *red nucleus*, *nucleus* or *locus ruber*. It is traversed by fibres of the third nerve as these make their way ventrally from the nucleus to the surface.

We must consider also as belonging to the tegmentum a large area of grey matter, somewhat lens-shaped in section (Fig. 114, *Sn*) which lies between the pes and tegmentum, sharply marking off the one from the other. From its dark appearance due to the abundance of black pigment it is called the *substantia nigra* or *locus niger*. It acquires its largest dimensions at about the middle of the length of the crus, coming to an end in front (Fig. 116, *Sn*) and fading away behind (Fig. 113) as the crus passes beneath the posterior corpora quadrigemina. These two, the red nucleus and the substantia nigra, are perhaps the most important collections of grey matter in the tegmentum, but we may add that at the front of the crus as the substantia nigra comes to an end there is seen in a somewhat similar position ventral to the hind part of the optic thalamus a collection of grey matter called the *corpus subthalamicum* (Fig. 116, *C.sb*).

At the hinder part of the crus, as it is about to plunge into the pons, while the pes, now decreasing relatively in size, still continues to be ordinary white matter composed of longitudinal bundles of medullated fibres, the tegmentum takes on more and more the structure which in speaking of the bulb we called reticular formation, and which, as we saw, deserves to be considered as a kind of grey matter.

The grey matter of the pons. When the conjoined crura as we trace them backward plunge beneath the pons the longitudinal fibres of the pes of each crus are as we have said soon split up into bundles scattered among the transverse fibres belonging to the pons itself. Dorsal to this system of transverse and longitudinal fibres forming the pons proper, between it on the ventral surface and the central grey matter with the posterior corpora quadrigemina on the dorsal surface, is a region which may be called tegmental since it is a continuation of the tegmentum of the crus. In the front part of the pons (Fig. 113), where the posterior corpora quadrigemina still form the dorsal roof of the section, this tegmental area, which is much broken up by certain strands of longitudinal fibres of which we shall speak later on, contains scattered nerve cells, and is largely composed of reticular formation. In this is placed on each side a group of nerve cells, the *locus caeruleus* (Fig. 113, *l.c.*), to which we have already referred (§ 621) as probably serving in part as the origin of the descending root of the fifth nerve (V. *d.*), just ventral to which it lies. This acquires larger dimensions farther back, in the front part of the fourth ventricle (Fig. 115, *l.c.*) between the levels represented in Figs. 112 and 113, and is a collection of large spindle-shaped nerve cells; it has a bluish tint when its black pigment is seen shining through the surrounding more or less transparent material, hence the name.

In the hinder parts of the pons (Figs. 111, 112) where the cerebellum is seen overhanging the open fourth ventricle, the reticular formation of the tegmental area is still more conspicuous. The only special collection of grey matter in this region to which we need call attention is one which, consisting like the olivary body of the bulb (or inferior olive) of a wall of grey matter surrounding and surrounded by white matter, is called the *upper olive* (Figs. 111, 112, *s.o.*).

The ventral part of the pons, or the pons proper, unlike the pes of the crus, contains mixed with the fibres a very considerable quantity of grey matter. This is fairly abundant in the front part of the pons (Fig. 113) below the corpora quadrigemina but increases even more behind this (Figs. 111, 112). Hence though the pons proper is largely built up of transverse and longitudinal fibres, and though it contains no compact aggregations of grey matter receiving special names, it does contain scattered throughout it a very large quantity of grey matter, far more indeed than is present in the tegmental portion; the grey matter of the pons, that is of the pons proper, must be regarded as forming a very important part of the grey matter of the crural system, and of no little physiological significance.

Behind the pons the crural system is continued into the bulb, with whose structure we have already dealt.

4. *Other Collections of Grey Matter.*

§ 630. Of these, three deserve chief attention, and may be classed together, though they differ in nature.

The grey matter of the corpora quadrigemina. On each side of and somewhat dorsal to the central grey matter of the aqueduct which, as we have seen, is well developed especially on the ventral side, collections of grey matter form the chief part of the corpora quadrigemina, both anterior and posterior.

The grey matter of the anterior corpora quadrigemina (Fig. 114, *A. Q. n*) is more distinctly marked off from, and separated by a wider tract of white matter from the central grey matter of the aqueduct than is that of the posterior corpora quadrigemina (Fig. 113, *nPQ*); it is moreover of a different nature. Indeed the two pairs of bodies have quite different relations, are of different nature, and perform different functions.

Corpora geniculata. The two optic nerves, as we shall see in detail later on, give rise, through the optic decussation, to the two optic tracts. Each optic tract (Figs. 108, 114, *Op*), winds round the crus cerebri on its ventral surface to reach the substance of the hemisphere in the region below the optic thalamus, and as it does so is described as dividing into a lateral and median portion. The lateral portion just as it sweeps round the far edge, that is the outer or lateral edge, of the crus bears a rounded swelling (Figs. 108 B and C, *C.gl.*) the *lateral* or *outer corpus geniculatum*, the interior of which consists largely of grey matter (Fig. 114, *Cgl*). The median portion similarly bears another like swelling occupying a more median position, the *median* or *inner corpus geniculatum* (Fig. 108 A and B, *Cgm*), the interior of which (Fig. 114, *Cgm*) also consists of grey matter. It is to be regretted that these two bodies should bear the same name, for they are different in their origin, in their connections, and in their functions. The lateral body is said to be derived from the forebrain, that is from the vesicle of the third ventricle, has definite connections with the retinal optic fibres, and is distinctly concerned in vision; the median body is derived from the midbrain, is not definitely connected with the retinal fibres, and appears to be in no way concerned in vision. We shall however return later on to the connections and probable functions of these bodies.

Corpus dentatum of the cerebellum. In the midst of the mass of white matter which is formed in the interior of the cerebellum by the confluence of the three peduncles, is found (Fig. 111, *CD*) an area of grey matter arranged, like the olivary body of the bulb, as a sharply folded or plaited band in the shape of a flask or bowl. As in the similar olivary body the grey wall of the flask is covered up by and its interior filled up with white matter; the mouth of the flask is on each side, directed towards the median line; the fibres pass chiefly to the superior peduncle.

There are also other collections of grey matter in the central white matter of the cerebellum, one of which, called the "nucleus of the roof," is connected with the two inferior peduncles.

The Arrangement of the Fibres of the Brain.

§ **631**. The systems, tracts and bundles of fibres in which the white matter of the brain is arranged, may be distinguished from each other, partly through mere mechanical separation by means of the scalpel, partly by being traced out with the help of the microscope, but, as in the spinal cord, much more fully and completely by differences of development, and by the method of degeneration.

We have seen that a marked feature of the brain is presented by the two crura cerebri which, running forward from the hind parts of the brain, spread out into each cerebral hemisphere. We have also seen that the crus in the wide sense of the word consists of two parts, a dorsal part, the tegmentum, and a ventral part, the pes or crusta, and that these two parts differ very strikingly from each other in structure and in relations. The pes consists exclusively of bundles of longitudinal fibres, and we may trace these from the cerebral hemispheres into the pons and some of them beyond the pons into the bulb and spinal cord. The tegmentum is more complex in structure; it consists of grey matter, and of fibres and bundles of fibres having various relations, both with the collections of grey matter lying within itself and with surrounding structures. It too has connections with the parts lying in front of it, and with the parts lying behind it; we may trace it too backwards through the pons into the bulb and forwards to the optic thalamus. If we allow ourselves to conceive of the optic thalamus as constituting the front ending of the tegmentum, we may arrange a large part of the brain into two main regions, into a tegmental region stretching from the optic thalamus through the dorsal portion of the pons to the dorsal portion of the bulb, and into a region, which we may call the pedal region, stretching from the internal capsule through the ventral portion of the pons to the ventral portion of the bulb.

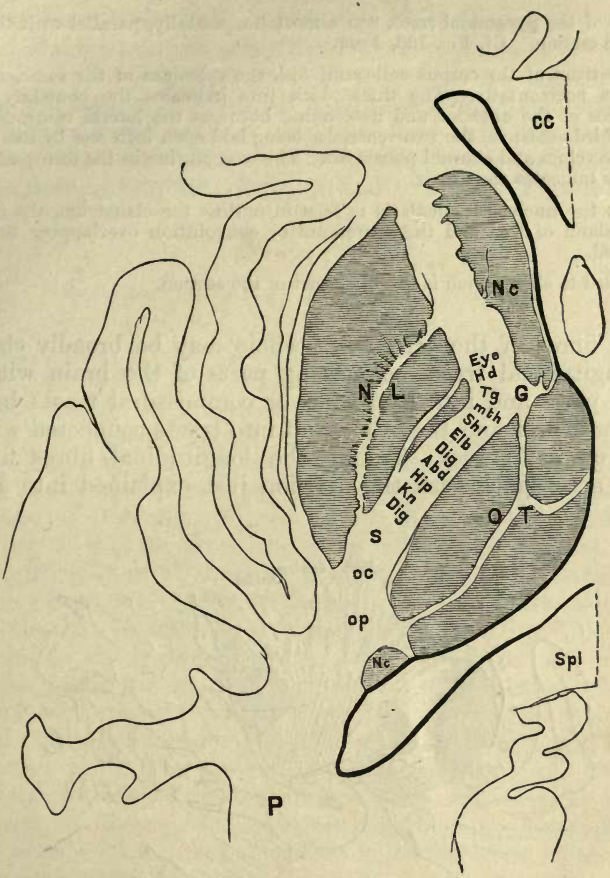

FIG. 121. OUTLINE OF HORIZONTAL SECTION OF BRAIN, TO SHEW THE INTERNAL CAPSULE. (Natural size.)

The section is taken at a level more ventral than shewn in Fig. 115. The grey matter of the cortex and claustrum is left unshaded, but that of the corpus striatum and optic thalamus is shaded.

OT. optic thalamus, shewing the median, lateral, and anterior nuclei. *NL*. nucleus lenticularis, shewing the putamen large, and the inner division of the globus pallidus very small. *NC*. nucleus caudatus, the large head in front of, and the diminishing tail behind, the thalamus.

G. the knee of the internal capsule. From '*Eye*' to '*Dig*,' marks the position of the pyramidal tract as a whole, and the several letters indicate broadly the relative positions of the several constituents of the tract, named according to the movements with which they are concerned; thus *Eye* movements of the eyes; *Hd*. of the head; *Tg*. of the tongue; *mth*. of the mouth; *shl*. of the shoulder; *elb*. of the elbow; *Dig*. of the hand; *Abd*. of the abdomen; *Hip*. of the hip; *Kn*. of the knee; *Dig*. of the foot.

S. the temporo-occipital tract. *oc*. fibres to the occipital lobe. *Op*. optic radiation. At this level the fibres of the frontal tract, in the fore limb of the capsule in front of the pyramidal tract, run almost horizontally, parallel with the plane of the section. Cf. Fig. 122, *Fron.*

cc. the rostrum of the corpus callosum, *Spl.* the splenium of the same, both cut across horizontally. The thick dark line indicates the boundary of the cavities of the anterior and descending horns of the lateral ventricle and of the third ventricle, the two ventricles being laid open into one by the removal of the velum and choroid plexus &c. The oval outline in the fore part of this cavity indicates the fornix.

Lateral to the nucleus lenticularis is seen in outline the claustrum, the cortex of the island of Reil and the operculum or convolution overlapping the island of Reil.

P is inserted to shew which is the hind part of the section.

The fibres of the brain as a whole may be broadly classified into longitudinal tracts connecting parts of the brain with succeeding parts and into transverse or commissural tracts between one lateral half and the other, and into tracts connected with the several cranial nerves. Taking the longitudinal fibres first we may in accordance with the division just explained into a pedal

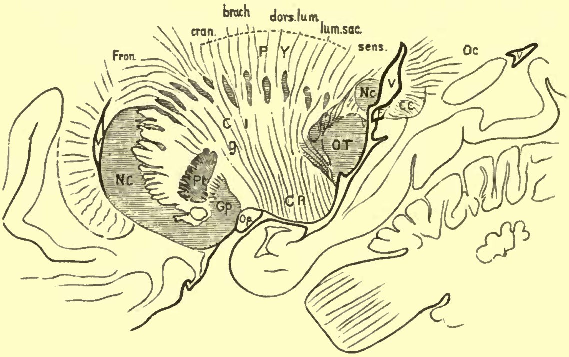

Fig. 122. Outline of a Sagittal section through the hemisphere. Man. (Sherrington.)

The section is taken not far to the right of the median plane and is one half linear of natural size. The grey matter of the corpus striatum and thalamus is shaded.

Nc, *Nc*, the caudate nucleus; *Pt*, the putamen and *Gp*, the globus pallidus of the lenticular nucleus; *OT*, the optic thalamus; *CI*, the internal capsule with a streaked appearance revealing approximately the direction taken by fibre-bundles passing into it from the portion of corona radiata over it. In these sets of bundles may be broadly distinguished a frontal system, *fron*, a pyramidal system, *PY* (sub-divisible into cranial (*cran.*), brachial (*brach.*), dorso-lumbar (*dors. lum.*), and lumbo-sacral (*lum. sac.*), parts) and a temporo-occipital system. *sens.*; the situation of the genu of the internal capsule is indicated by *g*. *CR*, the crus cerebri; *Oc*, the so-called optic radiations passing into the occipital lobe; *cc*, the splenial end of the corpus callosum; *v*, *v*, *v*, the lateral ventricle cut across in three different places; *F*, the fornix in cross-section; *Op*, the optic tract in cross-section. Part of the cerebellum is seen in outline to the right.

and a tegmental region, consider these as forming on the one hand a pedal, and on the other hand a tegmental system.

Both systems begin as we shall see in the cortex of the cerebral hemispheres. We shall have to deal with the topography of the cortex later on, but may here say that the first broad division of the whole surface of a hemisphere is into four main regions: frontal, parietal, occipital and temporal (Figs. 116, 117, 121).

Longitudinal fibres of the Pedal System.

§ **632**. *The pyramidal tract.* We have already (§ 575) said that the pyramidal tract of the spinal cord, may be traced to a particular region of the cerebral cortex. We shall study the details of this region, which is often spoken of as the "motor area" later on, but may here say that broadly speaking it is parietal in position and corresponds to the parts of the cortex gathered round the fissure of Rolando. Fibres passing from the grey matter of the cortex of this region to the white matter below, and so contributing their share to the central white matter of the hemisphere, converge (Figs. 122, 123) to form part of the internal capsule, namely that part which in a horizontal section (Fig. 121, *Eye* to *Dig*) occupies the knee and stretches for more than half, or nearly two-thirds, along the hind limb of the capsule, between the optic thalamus on the inside and the nucleus lenticularis on the outside. From the knee and hind limb of the capsule they pass by the side of and ventral to the optic thalamus (Figs. 116, 123), and so contribute to form the beginning of the crus cerebri. In thus converging to take up their position in the capsule and in their further passage to the crus the fibres follow a course of somewhat complicated curvature. As we trace the capsule from more dorsal to more ventral levels, we find it continually changing in form; the exact shape of the capsule shewn in Fig. 121 only holds good for the level at which the section was taken; it differs somewhat from that shewn in Fig. 115 taken at a slightly different level, and sections still more dorsal or still more ventral would present still greater differences. When we examine a series of horizontal sections, taken in succession from the dorsal to the ventral regions, we find that the knee shifts its position and changes in the width of its angle, that the two limbs vary in direction in size and in shape, and that at last the bent flattened capsule passes into the more or less rounded crus by the rapid disappearance of the fore limb, and the consequent extinction of the angle; so that in one sense it is the hind limb which becomes the crus, and the fibres of the fore limb may be said to pass into the crus through the ventral portion of the hind limb. Hence it is obvious that the fibres of the pyramidal tract, like the other fibres of the

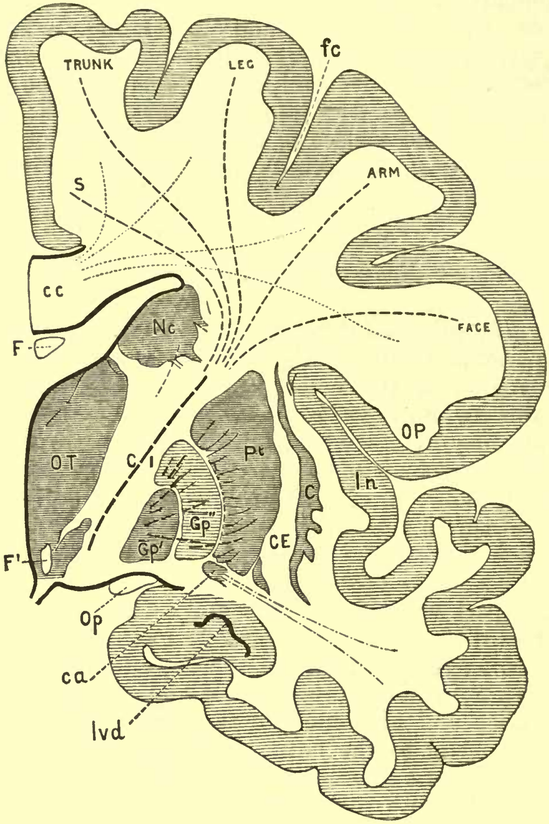

FIG. 123. OUTLINE OF A TRANSVERSE DORSO-VENTRAL SECTION OF THE RIGHT HALF OF THE BRAIN. (Natural size.) (Sherrington.)

The section which is taken at the level of the knee of the capsule and is therefore intermediate between those shewn in Figs. 116—117 is introduced to illustrate the course of the constituents of the pyramidal tract.

O.T. optic thalamus; *N.c.* nucleus caudatus, the head only appears in this section. *Pt.* putamen, *Gp''*, *Gp'* the two parts of the globus pallidus of the nucleus lenticularis; *C.* the claustrum; *C.E.* the external capsule; *In.* the island of Reil. *c.a.*, the anterior commissure shaded to render it distinct and the fibres from the temporo-sphenoidal lobe which pass into it being indicated by broken lines. *Op.* the optic tract; *lvd.* the end of the descending horn of the lateral ventricle; *F.* the fornix; *F'.* the end of the anterior pillar of the fornix in the base of the thalamus; *c.c.* corpus callosum; *OP.* anterior part of the occipital lobe.

f.c. is the central fissure or fissure of Rolando. The course of the fibres of the pyramidal tract connected respectively with the trunk, leg and arm, and hence with spinal nerves, and of those connected with the face and hence with cranial nerves, is shewn by broken lines. These are all seen converging into the internal capsule *C.I.* This figure should in respect to the course of these fibres be compared with the horizontal section shewn in Fig. 121, and the sagittal figure shewn in Fig. 122.

S. indicates the course of the most anterior and dorsal part of the temporo-occipital tract.

The fine dotted lines converging to the corpus callosum *c.c.* indicate the course of the callosal fibres.

capsule, are continually changing their direction as they pass through the capsule. Moreover while the fibres from different parts of the 'motor area' assume definite positions in relation to each other as they pass into the capsule, their relative positions are not constant, but vary somewhat. To this point however we shall return when we come to speak of the function of this tract.

In the crus these fibres run exclusively in the pes and form a compact strand (Fig. 114, *Py*) occupying the central and larger portion of the pes between a small median portion on the inside and a lateral portion on the outside. Maintaining this position along the crus they enter the pons, but here the previously compact strand is split up, by the interlacing transverse fibres of the pons, into a number of scattered bundles, which however as a whole still keep their central position. They form the greater part of but not all the bundles seen cut transversely in transverse sections of the pons (Figs. 112, 113). Farther backwards they become the pyramid of the bulb, and so give rise in the spinal cord to the direct and crossed pyramidal tracts. These fibres from the motor area of the cortex of the cerebrum are thus the source of the pyramidal tracts of the spinal cord, and hence the whole strand of fibres from the cortex downwards has been called the pyramidal tract. We have said (§ 575) that we have reasons for thinking that the pyramidal tract in the spinal cord makes connections through the grey matter of the anterior horn with the anterior roots of all the spinal nerves in succession; and similarly we have reason to think that along its course in the crus, in the pons, and in the bulb, before it reaches the cord, the tract also makes connections with the nuclei of those cranial nerves which are motor in function. During the passage of the tract through the internal capsule the fibres destined for cranial nuclei occupy the knee, while those belonging to the spinal cord run in the hind limb. Some authors limit the term pyramidal tract to the spinal moiety, since this alone forms the pyramid; but this is undesirable.

This tract is well marked out by the degeneration method, and the degeneration in it is a descending one, the trophic centres of the fibres being cells in the grey matter of the cortex. Removal of or injury to the cortex of the whole motor area gives rise to a degeneration along the whole tract, and removal of or injury to part of the area gives rise to degeneration of some of the strands. The tract is also well marked out by the embryological method; the fibres belonging to it acquire their medulla at times different from those of other fibres.

Anterior or frontal cortical. Fibres from the grey matter of the cortex in front of the motor area also pass to the internal capsule, but occupy the fore limb (Fig. 122, *fron*). Thence they pass to the crus, of which they form the small inner, median portion of the pes (Fig. 114, *Fr.*), and from the crus pass into the pons; in transverse sections of the pons they are seen as scattered bundles (Fig. 113, *F.C.*) to the median side of the pyramidal fibres. But here they seem to end; the degeneration of the tract is a descending one, and ceases here. Most probably the fibres end in the nerve cells of the grey matter, which as we have seen is abundant in the pons. It is also probable that through these nerve cells the fibres of this tract are connected with transverse fibres passing along the middle cerebellar peduncle into the cerebellum of the opposite side; but this has not been definitely proved.

Posterior or temporo-occipital cortical. Fibres from the grey matter of parts of the cortex behind the motor area also converge to the internal capsule, forming the hinder end of the hind limb behind the pyramidal tract (Fig. 121, *S*). These fibres also contribute to form the crus cerebri, passing into the pes, of which they occupy the outer lateral portion (Fig. 114, *Pr.O.*). From the crus they pass into the pons, where, like the fibres of the preceding tract, they appear to end, and probably in a like manner. This tract has been described as one of ascending degeneration, but in all probability like the preceding is one of descending degeneration.

The above three tracts of fibres may therefore all be regarded as starting from or having their trophic centres in the cortical grey matter of the hemispheres, as all helping to form, first the internal capsule and then the pes of the crus cerebri. But while the pyramidal tract passes, in part, to the spinal cord, the other two cease at the pons, and probably through the grey matter of the pons make connections with the cerebellum. Further while the pyramidal tract coming from the middle region of the cortex occupies a middle position in the capsule and a middle position in the crus, the system from the front part of the cortex occupies a front position in the capsule and an inner or median position in the crus and the system from the hind part of the cortex, a hind position in the capsule and an outer or lateral position in the crus. As the three systems pass from the cortex through the capsule to form the pes of the crus, their positions in relation to each other are shifted from one plane into another. As the fibres spread out from the pes through the capsule to all parts of the cortex, or, put in another way, as they converge from the cortex through the capsule to the pes, they form a fan, the corona radiata, which is not only curved, but the constituent parts of which cross each other.

Besides these three systems all passing from various regions of the cortex to the crus, there is yet a fourth strand contributed to the pes by the cerebral hemisphere though not starting in the cortex. *From the nucleus caudatus* fibres pass down to the crus, and take up a position in the pes dorsal to the tracts just mentioned, occupying a lens-shaped area immediately ventral to the substantia nigra, and probably passing into the substantia nigra itself. These cannot be traced farther down than the pons, where they appear to end, though possibly some terminate higher up in the substantia nigra. This tract has a descending degeneration, and may be regarded as a tract analogous to the front and hind cortical tracts, though it begins not in the cortex but in the nucleus caudatus; it is not however a very pure tract, many fibres of the pyramidal tract passing into it in the pes.

These are the main tracts of the pedal system. For, though the nucleus lenticularis gives off fibres to the internal capsule, our knowledge of the further course of these is at present imperfect, and though there seem to be longitudinal fibres connecting the bulb, the pons, and the pes at various levels, these are not numerous, and at all events do not form conspicuous strands.

Longitudinal Fibres of the Tegmental System.

§ **633**. *Cortical Fibres.* Although the fibres of the pedal system form, as we have seen, the greater part of, they do not form the whole of, the internal capsule. Fibres coming from all or nearly all parts of the cortex though they help to form the internal capsule, do not go on to form the pes, but pass to the optic thalamus (Fig. 116, *l.l.*) and appear to end in the grey matter of that body. In their passage through the capsule the fibres of this nature from the frontal and parietal regions of the cortex, occupy the extreme front end of the front limb in front of the frontal strand of the fibres of the pedal system (Fig. 121, *Th.*). The fibres from the occipital and temporal regions, those from the occipital regions being the most numerous and indeed being very conspicuous, occupy the extreme hind end of the hind limb of the capsule, behind the temporo-occipital division of the pedal system (Fig. 121, *Op.*). Since, as we shall see, we have reason to associate the occipital region of the cortex with vision, the fibres thus radiating to (or from) the thalamus through the extreme hind limb of the capsule from (or to) the occipital cortex have been called the *optic radiation.*

All the above tracts of fibres, though joining the thalamus and not passing on to the pes, take part in the formation of the internal capsule. But a considerable number of fibres coming from the temporo-occipital region and especially from the temporal region pass to the thalamus without joining the capsule; they pass ventral to and behind the pes as this plunges into the hemisphere to become the capsule, and so reach the thalamus.

We may here perhaps diverge for a moment to point out the contrast between the optic thalamus and the corpus striatum, or at least the nucleus caudatus. The former does not contribute to the pedal system, the latter supplies a marked contribution. The former receives fibres from all parts of the cortex; there are no such special contributions from the cortex to the latter. And this difference accords with the experience that when parts of the cortex are removed, or are congenitally absent, no degeneration or want of development is observed in the corpus striatum, while degeneration or want of development is observed in the optic thalamus as well as in parts of the pedal and tegmental systems. Hence, while we may regard the optic thalamus as an intermediate mass of grey matter receiving fibres from the cortex, and connecting the cortex with lower parts of the tegmental region, the corpus striatum, appears rather to be analogous to the cortex itself, to be a special modification of the cortex, sending fibres down into the pedal system, but itself receiving no special tracts of fibres from the cortex. Indeed we may probably regard the corpus striatum as the oldest part of the superficial grey matter of the hemisphere, the more ordinary cortex being a later development.

The tegmentum proper, lying ventral to the hind end of, and behind the thalamus, in which region as we have seen the conspicuous red nucleus is situated, is thus, by reason of its connection with the thalamus, indirectly connected with the cortex. But besides this, it has direct connections of its own with the cortex. Some of the fibres of the optic radiation, as well as fibres from the temporal and occipital regions described above as sweeping round the base of the internal capsule, are said to pass not to the thalamus, but to the tegmentum. Other fibres from the frontal and parietal regions traversing the lenticular nucleus in the sheets of white matter splitting the nucleus into parts, are also said to reach the tegmentum either by piercing through or by sweeping round the internal capsule. On their path these fibres are, according to some observers, joined by fibres coming from the lenticular nucleus itself, and possibly from the caudate nucleus, which fibres, on the view that these nuclei are modified cortex, may also be considered as cortical. Thus the forepart of the tegmental region is brought into ample connection with the cerebral hemisphere partly by fibres joining the thalamus, partly by fibres passing directly to the tegmentum proper.

The mode of degeneration of these cortical fibres of the tegmental system is at present a matter of dispute. Nor is the general nature of the fibres conclusively determined, though it is generally supposed that they carry impulses from the thalamus and parts of the tegmentum to the cortex.

§ **634**. In the tegmentum from the subthalamic region to the bulb the reticular formation is, as we have seen, more or less abundant; this, and the occurrence of various bundles of fibres, gives the region great complexity; and we must confine ourselves here to touching on one or two important longitudinal strands which traverse it.

The *superior peduncle of the cerebellum* is one of the most important of these. This is on each side a bundle of fibres which, taking origin chiefly from the grey matter of the nucleus dentatus, and the smaller neighbouring collections of grey matter, but also in part from the superficial grey matter, leaves the cerebellum in front of, and to the median side of the restiform body and passes forward towards the corpora quadrigemina to converge with its fellow. At first the two peduncles are superficial and dorsal in position (Figs. 111, 112, *S.P.*) and the space between them is bridged over by the valve of Vieussens (Fig. 112, *Vla*); but, still converging, they soon sink ventrally beneath the posterior corpora quadrigemina and at the level of the junction between the anterior and posterior corpora quadrigemina meet and decussate ventral to those bodies in the ventral region of the tegmentum (Fig. 113, *S.P.*). Beyond the decussation they are continued forwards in the tegmentum ventral to the anterior corpora quadrigemina as two strands, one on each side, which appear to end in the red nuclei.

In this way the peduncles connect certain parts of the grey matter of the cerebellum with the tegmental region, and more particularly with the red nucleus, and thus indirectly with the structures with which that region is itself connected.

The fillet. This, as we have seen (§ 612), takes origin in the bulb, in the interolivary layer between the inferior olives, from fibres which are derived through the supra-pyramidal or sensory decussation from the gracile and cuneate nuclei. From this origin it passes forward on each side as a flat band into the tegmental region of the pons, receiving accessions from the superior olive and other collections of grey matter, and dividing there into two strands, the median (Figs. 112, 113, *Fm*) and lateral (Figs. 112, 113, *Fl* and Fig. 108, *BF*) fillet. The lateral division ends partly in the grey matter of the posterior corpus quadrigeminum, and partly in the white matter underlying (Fig. 114, *dm*) the anterior corpus quadrigeminum; the median division passing farther forward appears partly to end in the grey matter of the anterior corpus quadrigeminum, but partly to be continued on to the subthalamic region of the tegmentum ventral to the thalamus, thence to the thalamus, and so to the cortex.

The longitudinal posterior bundles. In a transverse section through the fore part of the pons at the level of the posterior corpora quadrigemina a rather conspicuous bundle of longitudinal fibres (called the longitudinal posterior bundle) is seen on each side, cut transversely, in the dorsal region of the tegmentum just ventral to the nucleus of the fourth nerve (Fig. 113, *l*). Traced backward from the aqueduct beneath the fourth ventricle, it becomes less conspicuous (Fig. 112, *l*) though maintaining its position dorsal to the reticular formation, and at the hind end of the bulb appears to be a continuation forwards of those fibres, "ground fibres," of the anterior column of the cord which probably serve as successive short longitudinal commissures between the segments of the cord. While the somewhat analogous fillet runs ventral to the reticular formation, this posterior longitudinal bundle runs always dorsal to that structure. It may be traced forward as far as the nucleus of the third nerve, and is seen in transverse sections lying immediately ventral to that group of cells (Fig. 114, *l*.), but its further connections forward have not as yet been determined. It is relatively more prominent in the lower than in the higher animals, and its fibres acquire their medulla relatively early. It is supposed to be connected with the nuclei of the nerves governing the muscles of the eye, and so to be concerned in the movements of that organ.

Tracts from the corpora quadrigemina. From each corpus quadrigeminum there passes obliquely forwards and downwards on each side a band of fibres, connected with the grey matter of the corpus and known as its *brachium.* The anterior brachium (Fig. 114, *Ba*), as we shall see in dealing with the optic nerve, joins the lateral corpus geniculatum and helps to form the optic tract, but some of its deeper lying fibres proceed to the occipital cortex forming part of the fibres which we have (§ 633) described as passing from the occipital cortex to and past the thalamus. The posterior brachium passes to the median corpus geniculatum; having received fibres from, and probably given fibres up to that body, it is continued on to the tegmentum, and according to some authors through the tegmentum by the hind part of the hind limb of the internal capsule to the temporal region of the cortex, mingling in its course with fibres from the thalamus.

Transverse or so-called Commissural Fibres.

§ **635.** The two chief masses are those on the one hand belonging to the cerebrum, and those on the other hand belonging to the cerebellum.

In the cerebrum the most imposing mass of transverse fibres forms the *corpus callosum.* Starting from the cortex in nearly all parts of the hemisphere, the fibres converge towards the thick body of the corpus callosum placed in the middle line, and thence diverge to nearly all parts of the cortex of the hemisphere on the other side, interlacing in their course with the cortical fibres of the pedal and tegmental systems. It is supposed that by means of these fibres, each part of the cortex of one hemisphere is brought into connection with the corresponding part of the other hemisphere.

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Besides these callosal fibres from one hemisphere to another, the white matter of each hemisphere contains fibres called "association fibres," passing from one convolution to another of the same hemisphere.

The small *anterior white commissure* though it is placed in the front part of the third ventricle (Fig. 120, *A*) and, in part of its course, lies along the thalamus (Fig. 117, *Ca*) is really a commissure of particular parts of the cerebral hemispheres. A portion, very small in man, belongs to the olfactory tract; the rest takes origin on each side in a limited portion of the cortex (Fig. 116, *Ca*), which we shall later on speak of as the temporosphenoidal convolution and in which callosal fibres are deficient, whence it arches forward through the globus pallidus, past the thalamus (Figs. 123, *ca*, 117, *Ca*) to the front part of the third ventricle. It may be remarked that this commissure is still found in those lower animals which do not possess an obvious corpus callosum.

The small posterior commissure may be regarded as mainly a commissure between the two thalami, but it also helps to unite the tegmentum of the two sides and some fibres are said to pass on each side into the hemisphere. The middle or soft commissure of the third ventricle (Fig. 115, *c*), though it contains transverse fibres, is in the main a collection of grey matter, indeed a part of the central grey matter.

The *fornix*, together with, at all events, part of the septum lucidum which joins it with the corpus callosum, must also be regarded as a commissural structure. But its relations are peculiar; for while, behind, the diverging posterior pillars begin in the cerebral hemispheres, namely, in the walls of the descending horn of the lateral ventricle on each side, in front the anterior pillars or columns, leaving the cerebral hemispheres, pass along the lateral walls of the third ventricle (Fig. 120, *f*), and apparently end in the grey matter of the corpora albicantia. Whether the band of fibres, known as Vicq d'Azyr's bundle (Fig. 116, *Vb*), which running in the lateral wall of the third ventricle leads dorsally from each corpus albicans up to the anterior nucleus of the thalamus, is really to be considered as a continuation of the fornix is disputed; it may more probably be regarded as a part of the system spoken of above as connecting the cortex with the thalamus.

In the cerebellum true commissural fibres, are supplied by the *middle peduncles*; but by no means all the fibres of these peduncles are of this nature. The fibres of the middle peduncle, in contrast to those of the superior peduncle which start chiefly from the nucleus dentatus, or other internal grey matter, and to those of the inferior peduncle which start chiefly from the superficial grey matter of the vermis, appear to start from the superficial grey matter of the whole surface, from that of the median vermis as well as from that of the lateral hemispheres; they thus form the greater part of the central white matter. Sweeping down into the pons, they form the transverse fibres of that body, interlacing with the longitudinal fibres of the crural system and intermingling with the abundant grey matter.

Of these transverse fibres of the pons, a certain number are truly commissural; they make no connections with cells in the pons, but continue their way unbroken across it; they start in the superficial grey matter of one side of the cerebellum and end in the superficial grey matter of the other side, the parts of the grey matter thus united being probably corresponding parts. The most ventrally placed transverse fibres of the pons, which form a superficial layer of white matter, free from grey matter (Fig. 111, *tr. P.*) are probably of this nature, as are also the transverse fibres placed most dorsally, just ventral to the tegmental region.

A large number of the transverse fibres are not of this nature. They cross from one side of the cerebellum to the opposite side of the pons, but end in the pons apparently in the nerve cells of the grey matter; and it is supposed, that by these nerve cells they are brought into connection with the longitudinal fibres of the pedal system and thus with the cerebrum. They are transverse appendages of the pedal system, not true commissural fibres though they do cross the median line.

It is further supposed that other fibres of the middle peduncle reaching the pons do not cross the median line, but keeping to the same side and changing their direction, take a longitudinal upward course either with or without the intervention of nerve cells, and so make their way to the tegmentum. But this is not certain.

We must also consider as commissural structures the numerous fibres crossing, or serving to form the median raphe in the bulb. This raphe, with similar commissural fibres, is present in the tegmental portion of the pons, and indeed in the tegmentum itself.

Fibres also cross from one side to the other in connection with the cranial nerves, but these as well as all the tracts specially connected with the cranial nerves, including the olfactory and optic nerves, had better be considered by themselves.

Summary.

§ **636**. It may perhaps appear from the foregoing that the brain consists of a number of isolated masses of grey matter, some large, some small, connected together by a multitude of ties of white matter arranged in perplexing intricacy; and the addition of numerous collections of grey matter and strands of white matter of which we have made no mention would still further increase the perplexity. Nevertheless a systematic arrangement may be recognized, at least to a certain extent.

The least conspicuous, but perhaps in point of origin the oldest part of the brain, seems to be what we have called the central grey matter. This seems to serve chiefly as a bed for the development of the nuclei of the cranial nerves.

Next to the central grey matter and more or less associated with it comes what we have called the tegmental region, of which the reticular formation, coming into prominence in the bulb and continued on to the subthalamic region, forms as it were the core. Belonging to the tegmental system are numerous masses of grey matter from the conspicuous optic thalamus and the red nucleus in front to the several nuclei of the bulb behind. This complex tegmental system, which may perhaps be regarded as a more or less continuous column of grey matter, comparable to the grey matter of the spinal cord, serves as a sort of back bone to the rest of the central nervous system. With the spinal cord it is connected by various ties, besides being as it were a continuation of the spinal grey matter, and around it are built up the great mass of the cerebrum, and the smaller but still large mass of the cerebellum; the less important corpora quadrigemina we may for simplicity's sake neglect.

At the hind end we find various parts of the spinal cord becoming connected with this tegmental system, either passing into it and becoming, as far as our present knowledge goes, lost in it, or supplying strands or fibres which passing into it become through it connected with other parts. Thus the anterior column of the cord exclusive of the direct pyramidal tract, the lateral column exclusive of the crossed pyramidal and cerebellar tracts (and possibly the antero-lateral ascending tract), together with part of the posterior column appear to join the tegmental system, while part of the posterior column, after the relay of the gracile and cuneate nuclei, passes through the system as the fillet destined for various structures.

At the front end we find all parts of the cerebral cortex (though some regions, namely the temporo-occipital, to a greater extent than others), connected with the thalamus and other parts of the tegmental system; and, as we have seen, the corpus striatum may possibly possess like connections.

The relations of the cerebellum to this system are notable. On the one hand the cerebellum is directly connected with the system, partly by fibres which pass from the bulb to join the restiform body or inferior peduncle, partly by the superior peduncles which, as we have seen, are in a measure lost in the tegmentum, and partly probably by fibres of the middle peduncles also making connections with the tegmentum. On the other hand the cerebellum forms around the tegmental system a great junction between the spinal cord and the cerebrum. To the spinal cord it is joined in a direct manner by the cerebellar tract and possibly by the antero-lateral ascending tract, and in an indirect manner by the relay of the gracile and cuneate nuclei. To all parts of the cerebral cortex, it appears to be joined by those conspicuous strands of the pedal system, which, as we have seen, end in the pons, and there make connections with the fibres of the middle peduncle. And we may here perhaps remark that while this connection between the cerebrum and cerebellum is wholly a crossed one, each cerebral hemisphere being joined with the opposite half of the cerebellum, the connections between the spinal cord and the cerebellum are largely uncrossed ones, that by the cerebellar tract being wholly uncrossed, and that with the posterior column by the relay of the gracile and cuneate nuclei being in part uncrossed.

Thus the cerebral cortex has a double hold, so to speak, on the rest of the central nervous system first through the tegmental system, and secondly through the cerebellar junction. But in addition to this there is another tie between the cerebral cortex and the whole length of the cerebro-spinal axis, or at least between it and the whole series of motor mechanisms in succession from the nucleus of the third nerve to the nucleus, if we may so call it, of the anterior root of the coccygeal nerve, namely, the great pyramidal tract, which thus appears as a something superadded to all the rest of the central nervous system.

When the cerebral hemispheres are removed this pyramidal tract falls away as does also the pedal system leading from the cerebrum to the pons, but there still remains the tegmental system with its cerebellar and other adjuncts and this, as we shall see, constitutes a nervous machinery, capable of carrying out exceedingly complicated acts.

SEC. 4. ON THE PHENOMENA EXHIBITED BY AN ANIMAL DEPRIVED OF ITS CEREBRAL HEMISPHERES.

§ **637**. The cerebral hemispheres, as we have more than once insisted, seem to stand apart from the rest of the brain. In the case of some animals it is possible to remove the cerebral hemispheres and to keep the animal not only alive, but in good health for a long time, days, weeks, or even months after the operation. In such case we are able to study the behaviour of an animal possessing no cerebral hemispheres and to compare it with that of an intact animal. Such an experiment is best carried out on a frog. In this animal it is comparatively easy to remove the cerebral hemispheres, including the parts corresponding to the corpora striata, leaving behind intact and uninjured the optic thalami with the optic nerves, the optic lobes (or representatives of the corpora quadrigemina), the small cerebellum and the bulb. If the animal be carefully fed and attended to, it may be kept alive for a very long time, for more than a year for instance.

The salient fact about a frog lacking the cerebral hemispheres, is that, as in the case of a frog deprived of its whole brain, the signs of the working of an intelligent volition are either wholly absent or extremely rare. The presence of the bulb and the middle parts of the brain (for so we may conveniently call the cerebral structures lying between the cerebral hemispheres and the bulb) ensures the healthy action of the vascular, respiratory and other nutritive systems; food placed in the mouth is readily and easily swallowed; the animal when stimulated executes various movements; but if it be left entirely to itself, and care be taken to shield it from adventitious stimuli, either it remains perfectly and permanently quiescent, or the apparently spontaneous movements which it carries out are so few and so limited as to make it very doubtful whether they can fairly be called volitional. Such a frog, for instance, after being kept alive for some time and made to exhibit the phenomena of which we are about to speak, has been placed on a table with a line drawn in chalk around the area covered by its body, and left to itself has subsequently been found dead without having stirred outside the chalked circle.

We must here however repeat the caution laid down in § 582, as to the ultimate effects of an operation on the central nervous system. The longer the frog is kept alive and in good health after the removal of the cerebral hemispheres, the greater is the tendency for apparently spontaneous movements to shew themselves. For days or even weeks after the operation there may be no signs whatever of the working of any volition; but after the lapse of months, movements, previously absent, of such a character as to suggest that they ought to be called voluntary, may make their appearance. To this point we shall return, but may in the meanwhile state that even in their most complete development such movements do not negative the view that the frog in the absence of the cerebral hemispheres is wanting in what we ordinarily call a 'will.'

§ **638**. We have seen that a frog from which the whole brain has been removed and the spinal cord only left appears similarly devoid of a 'will;' but the phenomena presented by a frog possessing the middle portions of the brain differ widely from those presented by a frog possessing a spinal cord only. We may perhaps broadly describe the behaviour of a frog from which the cerebral hemispheres only have been removed, by saying that such an animal, though exhibiting no spontaneous movements, can by the application of appropriate stimuli be induced to perform all or nearly all the movements which an entire frog is capable of executing. It can be made to swim, to leap, and to crawl. Left to itself it assumes what may be called the natural posture of a frog, with the fore limbs erect, and the hind limbs flexed, so that the line of the body makes an angle with the surface on which it is resting. When placed on its back, it immediately regains this natural posture. When placed on a board, it does not fall from the board when the latter is tilted up so as to displace the animal's centre of gravity: it crawls up the board until it gains a new position in which its centre of gravity is restored to its proper place. Its movements are exactly those of an entire frog except that they need an external stimulus to call them forth. They differ moreover fundamentally from those of an entire frog in the following important feature; they inevitably follow when the stimulus is applied; they come to an end when the stimulus ceases to act. By continually varying the inclination of a board on which it is placed, the frog may be made to continue crawling almost indefinitely; but directly the board is made to assume such a position that the body of the frog is in equilibrium, the crawling ceases; and if the position be not disturbed the animal will remain impassive and quiet for an almost indefinite time. When thrown into water, the creature begins at once to swim about in the most regular manner, and will continue to swim until it is exhausted, if there be nothing present on which it can come to rest. If a small piece of wood be placed on the water the frog will, when it comes in contact with the wood, crawl upon it, and so come to rest. If disturbed from its natural posture, as by being placed on its back, it immediately struggles to regain that posture; only by the application of continued force can it be kept lying on its back. Such a frog, if its flanks be gently stroked, will croak; and the croaks follow so regularly and surely upon the strokes that the animal may almost be played upon like a musical, or at least an acoustic instrument. Moreover, provided that the optic nerves and their arrangements have not been injured by the operation, the movements of the animal appear to be influenced by light; if it be urged to move in any particular direction, it seems in its progress to avoid obstacles, at least such as cast a strong shadow; it turns its course to the right or left or sometimes leaps over the obstacle. In fact, even to a careful observer the differences between such a frog and an entire frog which was simply very stupid or very inert, would appear slight and unimportant except in this, that the animal without its cerebral hemispheres is obedient to every stimulus, and that each stimulus evokes an appropriate movement, whereas with the entire animal it is impossible to predict whether any result at all, and if so what result, will follow the application of this or that stimulus. Both may be regarded as machines; but the one is a machine and nothing more, the other is a machine governed and checked by a dominant volition.

Now such movements as crawling, leaping, swimming, and indeed, as we have already urged, to a greater or less extent, all bodily movements, are carried out by means of coordinate nervous motor impulses, influenced, arranged, and governed by coincident sensory or afferent impulses. Muscular movements are determined by afferent influences proceeding from the muscles and constituting the foundation of the muscular sense; they are also directed by means of afferent impulses passing centripetally along the sensory nerves of the skin, the eye, the ear, and other organs. Independently of the particular afferent impulses, which acting as a stimulus call forth the movement, very many other afferent impulses are concerned in the generation and coordination of the resultant motor impulses. Every bodily movement such as those of which we are speaking is the work of a more or less complicated nervous mechanism, in which there are not only central and efferent, but also afferent factors. And, putting aside the question of consciousness, with which we have here no occasion to deal, it is evident that in the frog deprived of its cerebral hemispheres all these factors are present, the afferent no less than the central and the efferent. The machinery for all the necessary and usual bodily movements is present in all its completeness. We may regard the share therefore which the cerebral hemispheres take in executing the movements of which the entire animal is capable, as that of putting this machinery into action or of limiting its previous activity. The relation which the higher nervous changes concerned in volition bear to this machinery may be compared to that of a stimulus, always bearing in mind that the effect of a stimulus on a nervous centre may be either to start activity, or to increase, or to curb, or to stop activity already present. We might almost speak of the will as an intrinsic stimulus. Its operations are limited by the machinery at its command. We may infer that in the frog, the action of the cerebral hemispheres in giving shape to a bodily movement is that of throwing into activity particular parts of the nervous machinery situated in the lower parts of the brain and in the spinal cord; precisely the same movement may be initiated in the absence of the cerebral hemispheres by applying such stimuli as shall throw precisely the same parts of that machinery into the same activity.

Very marked is the contrast between the behaviour of such a frog which, though deprived of its cerebral hemispheres, still retains the other parts of the brain, and that of a frog which possesses a spinal cord only. The latter when placed on its back makes no attempt to regain its normal posture; in fact, it may be said to have completely lost its normal posture, for even when placed on its belly it does not stand with its fore feet erect, as does the other animal, but lies flat on the ground. When thrown into water, instead of swimming, it sinks like a lump of lead. When pinched, or otherwise stimulated, it does not crawl or leap forwards; it simply throws out its limbs in various ways. When its flanks are stroked it does not croak; and when a board on which it is placed is inclined sufficiently to displace its centre of gravity it makes no effort to regain its balance, but falls off the board like a lifeless mass. Though, as we have seen, the various parts of the spinal cord of the frog contain a large amount of coordinating machinery, so that the brainless frog may, by appropriate stimuli, be made to execute various purposeful coordinate movements, yet these are very limited compared with those which can be similarly carried out by a frog possessing the middle and lower parts of the brain in addition to the spinal cord. It is evident that a great deal of the more complex machinery of this kind, especially all that which has to deal with the body as a whole, and all that which is concerned with equilibrium and is specially governed by the higher senses, is seated not in the spinal cord but in the brain. We do not wish now to discuss the details of this machinery; all we desire to insist upon at present is that, in the frog the nervous machinery required for the execution, as distinguished from the origination, of bodily movements even of the most complicated kind, is present after complete removal of the cerebral hemispheres, though these movements are such as to require the cooperation of highly differentiated afferent impulses.

§ 639. In warm-blooded animals the removal of the cerebral hemispheres is attended with much greater difficulties than in the case of the frog. Nevertheless, in the bird the operation may be carried out with approximate success. Pigeons for instance have been kept alive for five or six weeks after complete removal of the cerebral hemispheres, with the exception of portions of the crura and corpora striata immediately surrounding the optic thalami; these parts were left in order to ensure the intact condition of the latter bodies.

When the immediate effects of the operation have passed off, and for some time afterwards, the appearance and behaviour of the bird are strikingly similar to those of a bird exceedingly sleepy and stupid. It is able to maintain what appears to be a completely normal posture, and can balance itself on one leg, after the fashion of a bird which has in a natural way gone to sleep. Left alone in perfect quiet, it will remain impassive and motionless for a long time. When stirred it moves, shifts its position; and then, on being left alone, returns to a natural, easy posture. Placed on its side or its back it will regain its feet; thrown into the air, it flies with considerable precision for some distance before it returns to rest. It frequently tucks its head under its wings, and at times may be seen to clean its feathers; when its beak is plunged into corn, it eats. It may be induced to move not only by ordinary stimuli applied to the skin, but also by sudden loud sounds, or by flashes of light; in its flight it will, though imperfectly, avoid obstacles, and its various movements appear to be to a certain extent guided not only by touch but also by visual impressions.

In a certain number of cases this sleepy, drowsy condition passes off and is succeeded by a phase in which the bird, apparently spontaneously, without the intervention of any obvious stimulus, moves rapidly about. It does not fly, that is to say, it does not raise itself from the ground in flight, but walks about incessantly for a long while at a time, periods of activity alternating with periods of repose. It seems, from time to time, to wake up and move about, and then to go to sleep again; and it has been observed that during the night it appears to be always asleep. It is obvious, therefore, that the sleepy, quiescent condition is not due simply to the absence of the cerebral hemispheres, but is a temporary effect of the operation, and that spontaneous movements, that is to say, movements not started by any obvious stimulus, may occur after removal of the cerebral hemispheres. But the movements so witnessed differ from those of an intact bird. They are, it is true, varied; and the variations are in part dependent on external circumstances, the bird being guided by tactile, and as we have said, visual sensations, or, to be more exact, by impressions made upon the sensory nerves of the skin and on the retina; but they do not shew the wide variations of voluntary movements. The bird never flies up from the ground, never spontaneously picks up corn, and its aimless, monotonous, restless walks, resembling the continued swimming of the frog thrown into the water after being deprived of its cerebral hemispheres, forcibly suggest that the activity is the outcome of some intrinsic impulse generated in the nervous machinery in some way or other, but not by the working of a conscious intelligence as in the impulse which we call the will.

Still we must not shut our eyes to the fact that spontaneous movements, whatever their exact nature, are manifested by a bird in the absence of the cerebral hemispheres, and become the more striking the more complete the recovery from the passing effects of the mere operation. Could such birds be kept alive for any considerable time, possibly further developments might be witnessed, and indeed cases are on record where birds have been kept alive for months after the operation, and have shewn spontaneous movements of a still more varied character than those just described; but in such cases the removal of the hemispheres has not been complete, portions of the ventral regions being left behind; and, though a mere remnant left around the optic thalami can hardly be regarded as a sufficient cause for the spontaneity of which we are speaking, a larger mass, still more or less retaining its normal structure, might have a marked effect. And we may here perhaps remark that all these facts seem to point to the conclusion that what may be called mechanical spontaneity, sometimes spoken of as 'automatism,' differs from the spontaneity of the 'will' in degree rather than in kind. Looking at the matter from a purely physiological point of view (the only one which has a right to be employed in these pages), the real difference between an automatic act and a voluntary act is that the chain of physiological events between the act and its physiological cause is in the one case short and simple, in the other long and complex. We have seen that a frog lacking its cerebral hemispheres, viewed from one stand point, appears in the light of a mechanical apparatus, on which each change of circumstances produces a direct, unvarying, inevitable effect. And yet it is on record that such a frog, if kept alive long enough for the most complete disappearance of the direct effects of the operation, will bury itself in the earth at the approach of winter, and is able to catch and swallow flies and other food coming in its neighbourhood, although in other respects it shews no signs of an intelligent volition, and answers with unerring mechanical certainty to the play of stimuli. We may add that in some fishes the removal of their cerebral hemispheres, which in these animals form a relatively small part of the whole brain, produces exceedingly little change in their general behaviour.

These however are not the considerations on which we wish here to dwell; we have quoted the behaviour of the bird deprived of its cerebral hemisphere mainly to shew that in this warm-blooded animal, as in the more lowly cold-blooded frog, the parts of the brain below or behind the cerebral hemispheres constitute a nervous machinery by which all the ordinary bodily movements may be carried out. The bird, like the frog, suffers no paralysis when the cerebral hemispheres are removed; on the contrary, though its movements have not been studied so closely as those of the frog, the bird without its cerebral hemispheres seems capable of executing at all events all the ordinary bodily movements of a bird. And in the bird as in the frog, the afferent impulses passing into the central nervous system, whether they give rise to consciousness or no, play an important part not only in originating but in guiding and coordinating the efferent impulses which stir the muscles to contract, the coordination being effected partly in the spinal cord, but largely and indeed chiefly in the parts of the brain lying behind the cerebral hemispheres. It is further worthy of notice that spontaneity of movement of the kind which we have described, is much more prominent in the more highly developed bird, than in the more lowly frog. The cerebral hemispheres are not the only part of the central nervous system which has undergone a greater development in the bird; the other parts of the brain have also acquired a far greater complexity than in the frog.

§ **640.** In the mammal the removal of the cerebral hemispheres is still more difficult than in the bird; the animal cannot be kept alive for more than a few hours; but in some mammals it is possible to observe during those few hours phenomena kindred to those witnessed in the bird and in the frog. The rabbit or rat, from which the whole of both hemispheres has been removed with the exception of the parts immediately surrounding the optic thalami, can stand, run and leap. Placed on its side or back it at once regains its feet. Left alone it generally remains as motionless and impassive as a statue, save now and then when a passing impulse seems to stir it to a sudden but brief movement; but sometimes it seems subject to a more continued impulse to move, in which case death usually follows very speedily. Such a rabbit will remain for minutes together utterly heedless of a carrot or cabbage-leaf placed just before its nose, though if a morsel be placed within its mouth it at once begins to eat. When stirred it will with ease and steadiness run or leap forward; and obstacles in its course are very frequently, with more or less success, avoided. In some cases the animal (rat) has been described as following by movements of the head a bright light held in front of it (provided that the optic nerves and tracts have not been injured during the operation), as starting when a shrill and loud noise is made near it, and as crying when pinched, often with a long and seemingly plaintive scream. So plaintive is the cry which it thus gives forth as to suggest to the observer the existence of passion, this, however, is probably a wrong interpretation of a vocal action;

the cry appears plaintive simply because, in consequence of the completeness of the reflex nervous machinery and the absence of the usual restraints, it is prolonged.

Without insisting too much on such results as these, and allowing full weight to the objection which may be urged, that in some of these cases parts of the cerebral hemispheres surrounding the optic thalami were left, there still remains adequate evidence to shew that a mammal such as a rabbit, in the same way as a frog and a bird, may in the complete or all but complete absence of the cerebral hemispheres maintain a natural posture, free from all signs of disturbance of equilibrium, and is able to carry out with success, at all events all the usual and common bodily movements. And as in the bird and frog, the evidence also shews that these movements not only may be started by, but in their carrying out are guided by and coordinated by afferent impulses along afferent nerves, including those of the special senses. But in the case of the rabbit it is even still clearer than in the case of the bird that the effects of these afferent impulses are different from those which result when the impulses gain access to an intact brain. The movements of the animal seem guided by impressions made on its retina, as well as on other sensory nerves; we may perhaps speak of the animal as the subject of sensations; but there is no satisfactory evidence that it possesses either visual or other perceptions, or that the sensations which it experiences give rise to ideas. Its avoidance of objects depends not so much on the form of these as on their interference with light. No image, whether pleasant or terrible, whether of food or of an enemy, produces an effect on it, other than that of an object reflecting more or less light. And we may infer that it lacks the possession of an intelligent will. But it must always be remembered that some of the phenomena are due to the operation producing other results than the mere absence of the part removed. We must bear in mind that in all the above experiments while the positive phenomena, the things which the animal continues able to do, are of great value, the negative phenomena, the things which the animal can no longer do, are of much less, indeed of doubtful value. The more carefully and successfully the experiments are carried out, the narrower become what we may call the 'deficiency phenomena,' the phenomena which are alone and directly due to something having been taken away. Were it possible to keep the rabbit alive long enough for the mere effects of the operation to pass completely away, we should not only probably witness, as in the case of the bird a greater scope of movement and more frequent spontaneity, but possibly find a difficulty in describing the exact condition of the animal.

§ 641. Hitherto attempts to witness similar phenomena in more highly organised mammals such as the dog have failed; these animals do not recover from the operation of removing the whole of both their hemispheres sufficiently to enable us to judge whether they, like the frog, the bird and the rabbit, can carry out coordinate bodily movements in the absence of the hemispheres, or whether in them this part of the brain, so largely developed, has usurped functions which in the lower animals belong to other parts. Our knowledge is largely confined to the experience that when in a dog the cerebral convolutions are removed piecemeal at several operations, the animal may be kept alive and in good health for a long time, many months at least, even after these parts of the brain have been reduced to very small dimensions, and that under these circumstances, the animal is not only able to carry out with some limitations his ordinary bodily movements, but also exhibits a spontaneity obviously betokening the possession not merely of a conscious volition but of a certain amount of intelligence. Unless we are willing to believe that a mere fragment so to speak of the hemispheres can take on most extended powers, such an experience seems to shew that in the dog as in the rabbit and in the bird, the development of so-called higher functions is not limited to the cerebral hemispheres, that the middle and lower portions of the brain in the higher animals as compared with the lower do not increase in bulk merely as the instruments of the hemispheres, but like the hemispheres acquire more and more complex functions. We may perhaps go so far as to ask the question whether the volition and intelligence which such a dog exhibits is not as much the product of the parts lying behind the hemispheres as of the stump left in the front.

If we can thus say little about the condition of a dog without the cerebral hemispheres we can say still less about the monkey, which in all matters touching the cerebral nervous system serves as our best, indeed our only guide for drawing inferences concerning man; but in all probability the monkey in this respect bears somewhat the same relation to the dog that the dog bears to the bird.

In short, the more we study the phenomena exhibited by animals possessing a part only of their brain, the closer we are pushed to the conclusion that no sharp line can be drawn between volition and the lack of volition, or between the possession and absence of intelligence. Between the muscle-nerve preparation at the one limit, and our conscious willing selves at the other, there is a continuous gradation without a break; we cannot fix on any linear barrier in the brain or in the general nervous system, and say 'beyond this there is volition and intelligence but up to this there is none.'

This however is not the question with which we are now dealing. What we want to point out is that in the higher animals, including at least some mammals, as in the frog, after the removal of the cerebral hemispheres, even though conscious volition and intelligence appear to be largely, if not entirely, lost, the body is still capable of executing all the ordinary movements which the animal in its natural life is wont to perform, in spite of these movements necessitating the cooperation of various afferent impulses; and that therefore the nervous machinery for the execution of these movements lies in some part of the brain other than the cerebral hemispheres. We have reasons for thinking that it is situated in the structures forming the middle and hind brain; as we shall see, interference with these parts produces at once remarkable disorders of movement.

SEC. 5. THE MACHINERY OF COORDINATED MOVEMENTS.

§ **642.** We may now direct our attention for a while to some considerations concerning the nature of this complex nervous machinery for the coordination of bodily movements, and especially concerning the part played by afferent impulses. Most of our knowledge on this point has been gained by a study of animals not deprived of, but still possessing their cerebral hemispheres, or by deductions from the data of our own experience; but it is possible in most cases to eliminate from the total results the phenomena which are due to the working of a conscious intelligence. Some of the most striking facts bearing on this matter have been gained by studying the effects of operative interference with certain parts of the internal ear, known as the semicircular canals. The details of the structure of these parts we shall describe later on when we come to deal with hearing, but we may here say that each internal ear possesses three membranous semicircular canals, disposed in the three planes of space (one horizontal, and one in each of the two vertical planes, fore and aft and side to side), each membranous canal being surrounded by a bony canal of nearly the same shape, and being expanded at one end into what is called an ampulla, on which fibres of the auditory nerve end. Each membranous canal, in common with the cavity of the internal ear of which it is a prolongation, contains a fluid allied to lymph, called endolymph, and the space between each membranous canal and its corresponding bony canal is in reality a lymph space, containing a fluid which is virtually lymph, though it is called by the special name of perilymph. In birds interference with the semicircular canals produces the following remarkable results.

When in a pigeon the horizontal membranous semicircular canal is cut through, the bird is observed to be continually moving its head from side to side. If one of the vertical canals be cut through, the movements are up and down. The peculiar movements may not be witnessed when the bird is perfectly quiet, but they make their appearance whenever it is disturbed, or attempts in any way to stir. When the injury is confined to one canal only or even to the canals of one side of the head only, the condition after a while passes away; when the canals of both sides have been divided, it becomes much exaggerated, lasts much longer, and in some cases is said to remain permanently. After such injuries it is found that these peculiar movements of the head are associated with what appears to be a great want of coordination of bodily movements. If the bird be thrown into the air, it flutters and falls down in a helpless and confused manner; it appears to have lost the power of orderly flight. If placed in a balanced position, it may remain for some time quiet, generally with its head in a peculiar posture; but directly it is disturbed, the movements which it attempts to execute are irregular and fall short of their purpose. It has great difficulty in picking up food and in drinking; and in general its behaviour very much resembles that of a person who is exceedingly dizzy.

It can hear perfectly well, and therefore the symptoms cannot be regarded as the result of any abnormal auditory sensations, such as 'a roaring' in the ears. Besides, any such stimulation of the auditory nerve as the result of the section would speedily die away, whereas these phenomena may last for at least a very considerable time.

The movements are not occasioned by any partial paralysis, by any want of power in particular muscles or group of muscles; though removal of the canals of one side has been described as leading to diminished muscular force on the same side of the body, the mere diminution of force is insufficient to explain the phenomena. Nor on the other hand are the movements due to any uncontrollable impulse; a very gentle pressure of the hand suffices to stop the movements of the head, and the hand in doing so experiences no strain. The assistance of a very slight support enables movements otherwise impossible or most difficult, to be easily executed. Thus, though when left alone the bird has great difficulty in drinking or picking up corn, it will continue to drink or eat with ease if its beak be plunged into water, or into a heap of barley; the slight support of the water or of the grain seems sufficient to steady its movements. In the same way it can, even without assistance, clean its feathers and scratch its head, its beak and foot being in these operations guided by contact with its own body.

The amount of disorder thus induced differs in different birds; and some movements are more affected than others. As a general rule it may be said that the more complex and intricate a movement, the fuller and more delicate the coordination needed to carry it out successfully, the more markedly is it disordered by the operation; thus after injury to the canals, while a pigeon cannot fly, a goose is still able to swim.

In mammals (rabbits) section of the canals also produces a certain amount of loss of coordination, but much less than that witnessed in birds; and the movements of the head are not so marked, peculiar oscillating movements of the eye-balls, differing in direction and character according to the canal or canals operated upon, becoming however prominent. In the frog no deviations of the head are seen, but there is some loss of coordination in the movements of the body. In fishes no effect at all is produced.

Injury to the bony canals alone is insufficient to produce the symptoms; the membranous canals themselves must be divided or injured. The characteristic movements of the head may however be brought about in a bird without opening the bony canal, by suddenly heating or cooling a canal, especially its ampullar terminations, or by the making or breaking of a constant current directed through the canal.

There can be no doubt that these characteristic movements of the head are the result of afferent impulses started in the nervous endings of the auditory nerve over the ampulla of the canal, and conveyed to the brain along that nerve. And that injury to or other stimulation of each of the three canals should produce in each case a different movement of the head, the direction of the movement being different according to the plane in which the canal lies, shews that these impulses are of a peculiar nature. This is further illustrated by the following experiment. If the horizontal canal be carefully laid bare, and the membranous canal opened so as to expose the endolymph, blowing gently over the opened canal with a fine glass cannula will produce a definite movement of the head, which is turned to the one side or to the other, according as the current of air drives the endo-lymph towards or away from the ampulla. From this it is inferred that a movement of the endolymph over, or an increased pressure of the endolymph on, the nervous endings in the ampulla gives rise to afferent impulses which in some way determine the issue of efferent impulses leading to the movement of the head. It is further suggested that since the planes of the three canals lie in the three axes of space, any change in the position of the head must lead to changes in the pressure of the endolymph on the walls of the ampullae or to movements of endolymph over those walls, and so must give rise to impulses passing up the auditory nerve; and that since every change of position will affect the three canals differently (whereas the changes of pressure of the endolymph involved in a "wave of sound" will affect all three ampullae equally) those impulses will differ according to the direction of the change. A still further extension of this view supposes that since in any one position of the head the pressure of the endolymph will differ in the three ampullae, mere position of the head, as distinguished from change of position, is adequate to generate afferent impulses differing in the different positions.

Let us now for a while turn aside to ourselves and examine the coordination of the movements of our own bodies. When we appeal to our own consciousness we find that our movements are governed and guided by what we may call a sense of equilibrium, by an appreciation of the position of our body and its relations to space. When this sense of equilibrium is disturbed we say we are dizzy, and we then stagger and reel, being no longer able to coordinate the movements of our bodies or to adapt them to the position of things around us. What is the origin of this sense of equilibrium? By what means are we able to appreciate the position of our body? There can be no doubt that this appreciation is in large measure the product of visual and tactile sensations; we recognize the relations of our body to the things around us in great measure by sight and touch; we also learn much by our muscular sense. But there is something besides these. Neither sight nor touch nor muscular sense can help us when, placed perfectly flat and at rest on a horizontal rotating table, with the eyes shut and not a muscle stirring, we attempt to determine whether or no the table and we with it are being moved, or to ascertain how much it and we are turned to the right or to the left. Yet under such circumstances we are conscious of a change in our position, and some observers have been even able to pass a tolerably successful judgment as to the angle through which they have been moved. There can be no doubt that such a judgment is based upon the interpretation by consciousness of afferent impulses which are dependent on the position of the body, but which are not afferent impulses belonging to sensations of touch or sight, or taking part in the muscular sense. And it is urged with great plausibility that the afferent impulses in question are those which we have just referred to as started in the semicircular canals.

If we admit the existence of such ampullar impulses, if we may venture so to call them, and recognise them as contributing largely not only to our direct perception of the position of the head and thus of the body, but also in a more indirect way to what we have called the sense of equilibrium, we should expect to find that when they are abnormal the sense of equilibrium is disturbed, and that in consequence a failure of coordination in our movements results. And the loss of coordination which we described above as resulting from injury to the semicircular canals has accordingly been attributed to a deficiency or disorder of normal ampullar impulses.

But we must here distinguish between two things. It seems clear that when the membranous canals are injured or otherwise stimulated afferent impulses are generated which on the one hand may produce peculiar movements of the head, and on the other hand seem able when the injury is large to cause a loss of coordination of bodily movements. But it does not necessarily follow from this that in a normal condition of things afferent impulses are continually passing up to the brain from the semicircular canals, and that the loss of coordination which follows upon injury to the canals is due to these normal impulses being deficient or altered. It may be that such normal impulses do not exist, and that the loss of coordination is the result of the central machinery for coordination being interfered with by quite new impulses generated by the injury to the canal with the consequent loss of endolymph acting as a stimulus to the endings of the nerve. For the experience quoted above, though it proves that afferent impulses other than those of sight, touch and the muscular sense do reach the brain and afford a basis for a judgment as to the position of the body, does not by itself prove that those impulses come from the semicircular canals; the arrangement of the canals is undoubtedly suggestive; but it is quite possible that the afferent impulses in question may be generated by one or other of various changes, vaso-motor and others, of the tissues of the body which are involved in a change of position. And if it be true as affirmed by some observers that both auditory nerves may be completely and permanently severed, without any effect on the coordination of movements, it is obvious that the incoordination which follows upon section of the semicircular canals is due to some special irritation set up by the operation and not to the mere absence of any normal ampullar impulses. On the other hand, if the effects are those of irritation, it is difficult to understand how they can, as according to certain observers they certainly do, become permanent. It has however been strongly urged that in such cases of permanent incoordination, the operation has set up secondary mischief in the brain, in the cerebellum for instance, with which as we have seen (§ 618) the vestibular auditory nerve makes special connections, and that the permanent effects are really due to the disease going on here; and we have reason, as we shall see, to think that the cerebellum is concerned in the coordination of movements. It cannot therefore be regarded as settled that the canals are the source of normal impulses, or that our conscious appreciation of the position of the head and so of the body in space is based on such impulses. But such a view is not disproved; and in any case it remains true that injury to the canals does in some way or other, either by generating new impulses or by altering preexisting ones, so modify the flow of afferent impulses into the machinery of coordination as to throw that machinery out of gear.

§ **643**. We have dwelt on these phenomena of the semicircular canals because they illustrate in a striking manner the important part played by afferent impulses in the coordination of movements. We saw reason to think (§ 589) that even in an ordinary reflex movement carried out by the spinal cord or by a portion of the cord afferent impulses, other than those which excite the movement, are at work, determining such coordination as is present. In such a case the coordinating afferent impulses are relatively simple in character and start chiefly at all events in the muscles concerned. In an animal possessing the lower parts of the brain, though deprived of the cerebral hemispheres, the coordinating afferent impulses, in accordance with the greater diversity and complexity of the movements which the animal is able to execute, are far more potent and varied. Besides afferent impulses from the muscles, forming the basis of what we have called the muscular sense, afferent impulses from the skin, forming the basis of the sense of touch in the wide meaning of that word, other afferent impulses of obscure character from the viscera and various tissues, and the peculiar afferent ampullar impulses of which we have just spoken, important special afferent impulses borne along the nerves of sight and hearing come into play. The frog, the bird, and even the mammal, deprived of the cerebral hemispheres, though it may shew little signs or none at all of having a distinct volition, is as we have urged indubitably affected by visual and auditory impressions, and whether we admit or no that such an animal can rightly be spoken of as being conscious we cannot resist the conclusion that afferent impulses started in its retina or internal ear produce in its central nervous system changes similar to those which in a conscious animal form the basis of visual and auditory sensations, and we must either call these changes sensations or find for them some new word. Whatever we call them, and whether consciousness is distinctly involved in them or no, they obviously play an important part as factors of the coordination of movements. Indeed, when we appeal to the experience of ourselves in possession of consciousness, we find that though various sensations clearly enter into the coordination of our movements, we carry out movements thus coordinated without being distinctly aware of these coordinating factors. In every movement which we make the coordination of the movement is dependent on the impulses or influences which form the basis of the muscular sense, yet we are not distinctly conscious of these impulses; it is only as we shall see by special analysis that we come to the conclusion that we do possess what we shall call a muscular sense. So again, taking the matter from a somewhat different point of view, many of our movements, markedly as we shall see those of the eyeballs, are coordinated by visual sensations, and when we sing or when we dance to music our movements are coordinated by the help of sensations of sound. In these cases distinct sensations in the ordinary sense of the word intervene; if we cannot see or cannot hear, the movement fails or is imperfect; yet even in these cases we are not directly conscious of the sensations as coordinating factors; it needs careful analysis to prove that the success of the movement is really dependent on the sound or on the sight. These and other facts suggest the view that the point at which the various afferent impulses which form the basis of the sensations of a conscious individual enter into the coordinating mechanism is or may be some way short of the stage at which the complete conversion of the impulse into a perfect sensation takes place. The events which constitute what we may call visual impulses, as these leave the retina to sweep along the optic nerve, are we must admit very different from those which in the appropriate parts of the brain constitute what we may call conscious vision; and probably between the beginning and the end there are progressive changes. It is probable, we say, that these visual events may affect the coordinating mechanism at some stage of their progress before they reach their final and perfect form. If this be so we may further conclude that though, when the whole nervous machinery is present in its entirety, the afferent impulses which take part in coordination must inevitably at the same time give rise to conscious sensations, they might still effect their coordinating work when, owing to the imperfection or lack of the terminal part of the nervous machinery, the impulses failed to receive their final transformation, and conscious sensations were absent. In other words the coordinating influences of sensory or afferent impulses are not essentially dependent on the existence of a distinct consciousness.

§ 644. We have raised this point partly for the sake of illustrating the working of the coordination machinery in the absence of the cerebral hemispheres, but also in order to aid in the interpretation of the subjective condition which we speak of as giddiness or dizziness or vertigo. We compared the condition of the pigeon after an injury to the semicircular canals to that of a person who is giddy or dizzy, and indeed vertigo is the subjective expression of a disarrangement of the coordination machinery, especially of that concerned in the maintenance of bodily equilibrium. It may be brought about in many ways. When a constant current of adequate strength is sent through the head from ear to ear, we experience a sense of vertigo; our movements then appear to a bystander to fail in coordination, in fact to resemble those of a pigeon whose semicircular canals have been injured; and indeed the effects are probably produced in the same way in the two cases. In what is called Menière's disease attacks of vertigo seem to be associated with disease in the ear, being attributed by many to disorder of the semicircular canals, and cases have been recorded of giddiness as well as deafness resulting from disease of the auditory nerve. Visual sensations are very potent in producing vertigo. Many persons feel giddy when they look at a waterfall; and this is a case in which both the sense of giddiness and the disarrangement of coordination is the result of the action of a pure sensation and nothing else. In the well-known intense vertigo which is caused by rapid rotation of the body visual sensation plays a part when the rotation is carried on with the eyes open, but only a part; for vertigo may be induced, though not so readily, by rotation with the eyes completely shut. In the latter case it has been suggested that the vertigo is caused by abnormal ampullar impulses, but these can only contribute to the result which is in the main caused by direct disturbance of the brain. When the rotation is carried out with the eyes open, the vertigo which is felt when the rotation ceases is partly caused by the visual sensations, on account of the behaviour of the eyeballs, ceasing to be in harmony with the rest of the sensations and afferent impulses which help to make up the coordination. The rotation sets up peculiar oscillating movements of the eyeballs, which continue for some time after the rotation has ceased; owing to these movements of the eyeballs the visual sensations excited are such as would be excited if external objects were rapidly moving, whereas all the other sensations and impulses which are affecting the central nervous system are such as are excited by objects at rest. In a normal state of things the visual and the other sensations and impulses, which go to make up the coordinating machinery, are in accord with each other in reference to the events in the external world which are giving rise to them; after rotation they are for a time in disaccord, and the coordinating machinery is in consequence disarranged.

When we interrogate our own consciousness, we find that we are not distinctly conscious of this disaccord; the visual sensations are so prepotent in consciousness, that we really think the external world is rapidly whirling round; all that we are further conscious of is the feeling of giddiness and our inability to make our bodily movements harmonize with our visual sensations. So that even in the cases where the loss of coordination is brought about by distinct sensations what we really appreciate by means of our consciousness is the disarrangement of the coordinating machinery. It is the appreciation of this disorder which constitutes the feeling of vertigo; both the feeling of giddiness and the disordered movements are the outcome, one subjective and the other objective, of the same thing. It is not because we feel giddy that we stagger and reel; our movements are wrong because the machinery is at fault, and it is the faulty action of the machinery which also makes us feel giddy.

We may here perhaps remark that it is an actually disordered condition of the coordinating mechanism which gives rise to the affection of consciousness which we call giddiness, not a mere curtailing of the mechanism or any failure on its part to make itself effective. Complete blindness limits the range of activity of the machinery but leaves the remainder intact, and no giddiness is felt. So again in certain diseases of the nervous system the muscular sense is interfered with over considerable regions of the body, and in these regions coordination fails or is imperfect, but the central machinery is not thereby affected, though its area of usefulness is limited, and no giddiness is experienced; and so in other instances.

§ **645.** *Forced Movements.* So far we have dwelt on disorders of the coordinating machinery brought about by the action of various afferent impulses. We have now to call attention to some peculiar phenomena which result from operative interference with parts of the brain, and which in some instances at least may be taken to illustrate how this complex machinery works when some of its inner wheels are broken.

All investigators who have performed experiments on the brain have observed, as the result of injury to various parts of it, remarkable movements which have the appearance of being irresistible, compulsory, forced. They vary much in the extent to which they are developed; some are so slight as hardly to deserve the name, while others are strikingly intense. One of the most common forms is that in which the animal rolls incessantly round the longitudinal axis of its own body. This is especially common after section of one of the crura cerebri, or of the middle and inferior peduncles of the cerebellum, or after unilateral section of the pons, but has also been witnessed after injury to the bulb and corpora quadrigemina. Sometimes the animal rotates towards and sometimes away from the side operated on. Another form is that in which the animal executes 'circus movements,' *i.e.* continually moves round and round in a circle of longer or shorter radius, sometimes towards and sometimes away from the injured side. This may be seen after several of the above-mentioned operations, and in one form or another is not uncommon after various unilateral injuries to the brain. There is a variety of the circus movement, "the clockhand movement," said to occur frequently after lesions of the posterior corpora quadrigemina, in which the animal moves in a circle, with the longitudinal axis of its body as a radius, and the end of its tail for a centre. And this form again may easily pass into a simple rolling movement. In yet another form the animal rotates over the transverse axis of its body, tumbles head over heels in a series of somersaults; or it may run incessantly in a straight line backwards or forwards until it is stopped by some obstacle. These latter forms of forced movements are sometimes seen after injury to the corpus striatum even when a very limited portion of the grey matter is affected. And many of these forced movements may result from injuries which appear to be confined to the cerebral cortex.

When the phenomena are well developed, every effort of the animal brings on a movement of this forced character. Left to itself and at rest the animal may present nothing abnormal, its posture and attitude may be quite natural; but when it is excited to move or when it attempts of itself to move, it executes not a natural movement but a forced one, turning round or rolling over as the case may be. In severe cases the movement is continued until the animal is exhausted; when the exhaustion passes off the animal may remain for some little time quiet, but some stimulus, intrinsic or extrinsic, soon inaugurates a fresh outbreak, to be again followed by exhaustion.

In some of the milder forms, that for instance of the circus movement with a long radius, the curved character of the progression appears simply due to the fact that in the effort of locomotion volitional impulses do not gain such ready access to one side of the body as to the other, the injury having caused some obstacle or other. Hence the contractions of the muscles of one side (the left for instance) of the body are more powerful than the other, and in consequence the body is continually thrust towards the other (the right) side. As is well known we ourselves, when our walk is not guided by visual sensations, tend to describe a circle of somewhat wide radius, the deviation being due to a want of bilateral symmetry in our limbs; and the above circus movement is only an exaggeration of this.

But the other more intense forms of forced movements are more complicated in their nature. No mere blocking of volitional impulses will explain why an animal whenever it attempts to move rolls rapidly over, or rushes irresistibly forwards or backwards. It is not possible with our present knowledge to explain how each particular kind of movement is brought about; and indeed the several kinds are probably brought about in different ways, for they differ so greatly from each other that we only class them together because it is difficult to know where to draw the line between them. But we may regard the more intense forms as illustrating the complex nature of what we have called the coordinating machinery, the capabilities of which are, so to speak, disclosed by its being damaged. Such gross injuries as are involved in dividing cerebral structures or in injecting corrosive substances into this or that part of the brain, must, of necessity, partly by blocking the way to the impulses which in a normal state of things are continually passing from one part of the brain to another, partly by generating new unusual impulses, seriously affect the due working of the general coordinating machinery. The fact that an animal can, at any moment, by an effort of its own will, rotate on its axis or run straight forwards, shews that the nervous mechanism for the execution of those movements is ready at hand in the brain, waiting only to discharged; and it is easy to conceive how such a discharge might be affected either by the substitution for the will of some potent intrinsic afferent impulse or by some misdirection of volitional impulses. Persons who have experienced similar forced movements as the result of disease report that they are frequently accompanied, and seem to be caused, by disturbed visual or other sensations; thus they attribute their suddenly falling forward to the occurrence of the sensation that the ground in front of them is suddenly sinking away beneath their feet. Without trusting too closely to the interpretations the subjects of these disorders give of their own feelings, and remembering what was said above concerning vertigo, we may at least conclude that the unusual movements are in many cases due to a disorder of the coordinating mechanism, brought about by strange or disordered sensory impulses. And this view is supported by the fact that many of these forced movements are accompanied by a peculiar and wholly abnormal position of the eyes, which alone might perhaps explain many of the phenomena.

§ **646.** The phenomena presented by animals deprived of their cerebral hemispheres shew that this machinery of coordination is supplied by cerebral structures lying between the cerebral hemisphere above and the top of the spinal cord below. But when we ask the further question, how is this machinery related to the various elements which go to make up this part of the brain? the only answers which we receive are of the most imperfect kind.

In the case of the frog we can, after removal of the cerebral hemispheres, make an experimental distinction in the parts left between the optic thalami with the optic nerves and tracts, the optic lobes, and the bulb with the rudimentary cerebellum. When the optic thalami are removed, as might be expected, the evidence of visual impressions modifying the movements of the animal disappears; and it is stated that apparently spontaneous movements are much more rare than when the thalami are intact. When the optic lobes as well as the cerebral hemispheres are removed, the power of balancing is lost; when such a frog is thrown off its balance by inclining the plane on which it is placed, it slips back or falls down; the special coordinating mechanism for balancing must therefore in this animal have a special connection with the optic lobes. But after removal of these organs the animal is still capable of a great variety of coordinate movements: unlike a frog retaining its spinal cord only, it can swim and leap, it maintains a normal posture, and when placed on its back immediately regains the normal posture. The cerebellum of the frog is so small, and in removing it injury is so likely to be done to the underlying parts, that it becomes difficult to say how much of the coordination apparent in a frog possessing cerebellum and bulb is to be attributed to the former or to the latter; probably, however, the part played by the former is small.

In the case neither of the bird nor of the mammal have we any exact information as to the behaviour of the animal after removal of the parts behind the hemispheres, in addition to the hemispheres themselves. Our knowledge is confined to the results of the ablation, or of the stimulation of parts, the cerebellum for instance, in animals in which the rest of the brain has been left intact. Observations of this kind have disclosed many interesting facts, besides the forced movements just referred to, but they have not led to, and indeed could hardly be expected to lead to, any clear views as to the point which we are now discussing. It does not follow that every part, injury or stimulation of which interferes with coordinated movements, or gives rise to definite, forced, or other movements, is to be considered as part of the machinery under consideration. The corpora striata and cerebral hemispheres form, as we have seen, no part of the machinery, yet injury to them may disorder the machinery; and the fact that removal of, or injury to the cerebellum, disorders the machinery is no proof by itself that the cerebellum is an essential part of the machinery.

If we may trust to deductions from structural arrangements, we might be inclined to infer that the anatomical relations of what we have called the tegmental region from the bulb upwards point to its serving as the foundation of the machinery in question. Behind, it has full connections with various parts of the cord, while in front by means of the optic thalami and anterior corpora quadrigemina, if not by other ways as well, it is so far associated with the optic nerves that the path seems open for visual impulses to gain access to it. To this foundation, however, we must add the cerebellum, on account of its relations to it, to the cord and to the bulb through the restiform bodies, including its ties with the auditory nerve. And if we add the cerebellum we must also probably add the pons. We may exclude the pes of the crus, since this is composed exclusively of fibres bringing the cerebral hemispheres, including the corpora striata, into connection with the pons, bulb and cord, and so with the coordinating machinery itself, as well as with other parts of the nervous system. And observation as far as it goes supports this deduction from anatomical relationships. We will, however, defer what else we have to say on this point until after we have discussed the carrying out of voluntary movements.

SEC. 6. ON SOME HISTOLOGICAL FEATURES OF THE BRAIN.

§ **647**. The white matter of the brain, as we have already said, like that of the spinal cord consists of medullated fibres, of various sizes, imbedded in neuroglia and supported by septa of connective tissue derived from the pia mater. Save that cells, or even groups or rows of cells, for the most part small cells, about many of which it may be debated whether they are nerve cells or neuroglia cells, are frequently seen between the fibres and bundles of fibres, the white matter of the brain seems essentially identical with that of the spinal cord.

The grey matter of the brain in general also corresponds to the grey matter of the cord in consisting of branching nerve cells, fine medullated fibres of peculiar nature, non-medullated fibres and fibrils, with a few ordinary medullated fibres, all supported in neuroglia.

The 'central' grey matter is extremely like that of the cord except that the nervous elements are imbedded in a relatively larger quantity of neuroglia. Immediately underneath the epithelium lining the several ventricles and the aqueduct, the neuroglia is especially developed, forming a distinct layer which may be regarded as a continuation of the central gelatinous substance of the spinal cord, and which with the epithelium overlying it forms what is known as the *ependyma.* The 'nuclei' of the cranial nerves are as we have seen comparable to the groups of nerve cells in the spinal cord.

A great deal of the grey matter of the brain may be spoken of as more 'diffuse' or 'scattered,' more broken up by bundles of fibres than is the case in the spinal cord. The 'reticular formation' of the bulb, and of the tegmental region, is an extreme form of this diffuse grey matter. And even in such collections of indubitable grey matter as the corpus striatum, optic thalamus and the like, the pure grey matter, if we may use the term, is much more interrupted and broken up by conspicuous bundles of white fibres than is the case in any region of the spinal cord. In the corpora quadrigemina too the grey matter is broken up by sheets or bundles of white matter.

The nerve cells of the several collections of grey matter are not all alike; they present in different regions differences in size, form, and in other characters. The cells of the nucleus caudatus, for instance, are rather small and often round or spindleshaped, while those of the optic thalamus are large, branched and rich in pigment. The cells of the substantia nigra are spindleshaped, of moderate size, and so loaded with black pigment (in man) as to justify the name; those of the locus caeruleus are very large and spherical, with just so much pigment as to give a blueish tint. But our knowledge of the finer histological details of the various masses of grey matter is at present too imperfect to afford any basis whatever for physiological deductions; and it will be hardly profitable to dwell upon them. Two regions of grey matter alone call for special description, the cortex cerebri and the superficial grey matter of the cerebellum.

The superficial grey matter of the cerebellum.

§ 648. The surface of the cerebellum is increased by being folded or plaited into leaf-like folds, and each of these primary folds is similarly folded into a number of secondary, also leaf-like, folds or lamellae. Each of these lamellae consists of a central core of white matter, the fibres of which pass inwards to, and contribute to form the central white matter of the cerebellum, and of a superficial layer of grey matter. A section through a lamella perpendicular to the surface shews that the grey matter consists essentially of two layers: a layer lying next to the white matter formed by densely crowded small cells, called the *nuclear layer*, and between this and the superficial pia mater a much thicker layer of peculiar nature, called the *molecular layer*. Between these two layers, and connected as we shall see with both of them, lies a row of very large and remarkable cells, called *the cells of Purkinjé*, the bodies of which abut on the nuclear layer, and the long branches of which traverse the molecular layer; these cells so placed may be said to constitute a third layer. Before proceeding further, we may here remark that a section of the lamella, that is one of the secondary not one of the primary folds, while still remaining a vertical section (that is perpendicular to the surface) may be carried through the lamella in different planes, and that of these several planes, the sections taken in two of them are especially instructive, namely, the one taken in what we may call the longitudinal plane, passing from the top of the lamella to its base, and the one taken at right angles to the former, in what we may call the transverse plane. The nuclear layer and the molecular layer present the same broad features in both longitudinal and transverse sections, but the long branched processes of the cells of Purkinjé since they run in the transverse plane are adequately seen in transverse sections only, longitudinal sections shew only their profiles.

The molecular layer is of a peculiar nature. In many modes of preparation and in many sections it appears chiefly composed of a granular or dotted ground substance; hence the name molecular, as if it were an aggregation of molecules. The dots however are sections of fine fibrils, some of which are neuroglia fibrils but others are undoubtedly nervous. The layer consists in fact partly of a bed of neuroglia and partly of nervous elements, and here perhaps even more than elsewhere it is extremely difficult to say with regard to many of the elements whether they are neuroglial or nervous in nature. A considerable portion of the whole area of the molecular layer is taken up by the conspicuous branched processes of the cells of Purkinjé; and scattered about lie numerous small cells, some of which are neuroglia cells, but some of which are undoubtedly nerve cells. The most conspicuous feature of the layer however is the presence in large numbers of the fine fibrils; but before we speak of these it will be desirable to turn to the cells of Purkinjé and the nuclear layer.

The cell of Purkinjé possesses a large ($40\ \mu$ by $30\ \mu$) flask-shaped body, surrounding a large conspicuous clear, rounded, nucleus; it has much the appearance of a large ganglion cell. The base of the flask rests on the nuclear layer, and from it there proceeds a single axis cylinder process which passing through the nuclear layer somewhat obliquely, and in its passage acquiring a medulla, joins the central white substance as a medullated fibre. The cells as we have said form a single layer only, but since this covers the nuclear layer over the whole of the lamella, a considerable number of the fibres of the white central matter, though only a very small fraction of the whole, are thus derived from these cells of Purkinjé. The narrowed neck of the flask running outward in the molecular layer divides in an arborescent fashion into a large number of branches which, spreading out laterally in the transverse plane and stretching as far as the surface, ramify through the molecular layer, and are eventually lost to view as exceedingly fine fibrils. Some observers maintain that some of the fine processes are continuous with processes of the small nerve cells of the molecular layer, but this is not admitted by all. In any case the fibrillar terminations of these cells of Purkinjé contribute to the fine fibrils of the molecular layer.

The nuclear layer in ordinary stained specimens has the appearance of a mass of nuclei closely crowded together in a bed of reticular nature; and since the nuclei usually stain deeply, the layer stands out in strong contrast to the much less deeply stained molecular layer. Careful examination with special modes of preparation shews however that while some of the nuclei are nuclei belonging to neuroglia and blood vessels, the majority belong to small nerve cells of a peculiar nature. In these cells the nucleus is surrounded by cell substance which, forming a thin layer immediately around the nucleus, is chiefly disposed as thin spreading branches, some of which end in a peculiar arborescence not unlike a muscle end-plate; these processes contribute with the neuroglia to form the reticular looking bed spoken of above. No process can be traced inwards to the central white matter; but one of the processes gives off a branch, which passing vertically outwards takes on the appearance of a delicate axis cylinder process and runs, without dividing, into the molecular layer for a variable distance, sometimes reaching close to the surface, but at last divides at right angles into two fibrils, which run in the longitudinal plane in opposite directions for a considerable distance, and are ultimately lost to view. Since these cells in the nuclear layer are very numerous and each gives rise in the above manner to longitudinal fibrils, the molecular layer is traversed by a multitude of fibrils, visible as such in longitudinal sections but appearing as dots in transverse sections, in which the cells of Purkinjé are best displayed.

Besides these longitudinal fibrils proceeding from the cells of the nuclear layer, special modes of preparation similarly disclose numerous transverse as well as more or less oblique fibrils. Many of these appear to result from the branching of the small nerve cells of the molecular layer, and some of those so arising descend to the layer of the cells of Purkinjé and end around the bodies of those cells in remarkable nests of fibrils, without however actually making connections with them.

The medullated fibres of the central white matter of a lamella pass on all sides into the nuclear layer; or, put in another way, medullated fibres passing out of the nuclear layer at all points converge to form the central white matter. Some of these fibres as we have seen begin, or end, in the cells of Purkinjé. None of them appear to join the cells of the nuclear layer, and we have no evidence that any of them end or begin in any way in the nuclear layer. A certain number, however, may be seen to pass through the nuclear layer and between the cells of Purkinjé into the molecular layer, where losing their medulla they divide and apparently contribute to the numerous fibrils of the molecular layer. The presumption therefore is that all the fibres of the white matter begin or end either in the cells of Purkinjé or the fibrils of the molecular layer.

The superficial grey matter of the cerebellum then resembles the grey matter of the spinal cord in so far as it consists of branching nerve cells, nerve fibres, and nerve fibrils embedded in neuroglia; but the disposition and features of the several factors are peculiar. We may take perhaps as the key of the structure the fibrils of the molecular layer; this layer is relatively very thick, about 400 μ, much thicker than the nuclear layer which, however, varies in thickness, being generally thickest at the top of the fold; hence the number of fibrils in it may be spoken of as enormous. These fibrils seem certainly to be connected on the one hand with the cells of the nuclear layer and on the other hand with the scattered small cells of their own layer; but we have no evidence that these two sets of fibrils are continuous with each other; on the contrary, it seems more probable that the two sets of cells represent two independent systems. We can hardly doubt that these fibrils are in functional connection with the medullated fibres of the central white matter; but we have no clear evidence that the system of scattered cells is continuous either with the cells of Purkinjé, and so with the medullated fibres belonging to those cells, or with the medullated fibres which end independently in the molecular layer; and we have no evidence at all that the system of the cells of the nuclear layer is connected with either. We can hardly think otherwise than that the molecular changes which sweep to and fro along the tangle of these fibrils (whose nutrition is probably governed and hence whose functional activity is probably regulated by the nuclear and scattered cells respectively) are influenced by or originate the nervous impulses passing along the medullated fibres of the white matter; and hence we must conclude that either a continuity exists which has as yet escaped detection or, what is quite possible if not probable, that one fibril can act upon another by simple contact or even at a distance. Further, while the cell of Purkinjé, with its large cell body and nucleus, its conspicuous axis cylinder process and its other branched processes presents many analogies with a motor cell, such as those of the anterior horn of the spinal cord, and raises the presumption that the impulses which move along its axis-cylinder process, proceed outwards from the cell as motor or at least as efferent impulses, we have no direct proof that this is so. And though it is tempting to suppose that the other medullated fibres, which like the fibres of a posterior root are lost in the grey matter, without the intervention of a conspicuous cell, carry afferent impulses, we have as yet no proof of this. All we can say is that the grey matter is connected in two different ways with at least two sets of fibres, which probably therefore have different functions.

We may here add the remark that the large body of the cell of Purkinjé lies, as indeed do the other nervous elements, in an appropriate space in the bed of neuroglia. Between the surface of the cell and the wall of neuroglia is a space, generally so narrow as to be potential rather than actual, but which may sometimes be considerable. Whether small or large it contains lymph, and the cavity in which the cell lies is in connection with the lymphatics of the brain. Each cell then lies in a lymph space; but we merely mention the fact now; we shall have to return to the matter when we come to deal with the lymphatic and vascular arrangements of the brain and spinal cord.

The Cerebral Cortex.

§ **649**. While the superficial grey matter of the cerebellum does not differ strikingly as to its histological features in different regions, very considerable differences are observed in different regions of the cerebral cortex. A general plan of structure may perhaps be recognized, but as we pass from one part of the cerebra surface to another we find modifications continually taking place. We must content ourselves here with attempting a description of the general plan followed by an indication of the more striking characteristics of certain regions.

The cortical grey matter, having an average thickness of about 3 mm., but varying considerably in different regions from 1·8 mm. in some parts of the occipital lobe to 4·2 at the dorsal summit of the precentral convolution, is, like other grey matter, composed of nerve cells, and of nerve fibres and fibrils supported by neuroglia. The nerve cells, at least the conspicuous and easily recognized nerve cells, are scattered, and appear, in sections, to be imbedded in, and separated from each other by a not inconsiderable but variable quantity of somewhat peculiar ground substance, not unlike that which forms so large a part of the molecular layer of the cerebellum. Part of this ground substance, which apparently is not confined to any particular layer, but stretches throughout the thickness of the cortex is undoubtedly neuroglial in nature, but part, and probably the greater part, is nervous in nature; it is largely composed of fine fibrils traversing it in various directions, the transverse sections of these fibrils giving it a characteristic dotted or 'molecular' appearance; and the majority of these fine fibrils are probably the continuations of branching nerve cells or dividing nerve fibres, the remainder being neuroglial fibrils. In this respect it resembles the molecular layer of the cerebellum, but it is, to a much greater extent than is that layer, traversed by medullated nerve fibres, especially by fine medullated fibres like those seen in the grey matter of the spinal cord, § 563.

The nerve cells imbedded in this ground substance in more or less distinct layers are of various kinds. The most conspicuous, abundant and characteristic nerve cells found in the cortex of all regions of the cerebrum, are those which from their shape are called *pyramidal cells.* These vary much in size and have been distinguished as 'small pyramidal' cells averaging 12 μ in length by 8 μ in breadth, and 'large pyramidal' cells, sometimes called 'ganglionic cells,' of which the medium size is about 40 μ in length by 20 μ in breadth. Some of the latter, occurring in special regions are of very large size, 120 μ by 50 μ and have been called 'giant cells.'

The features of a 'large pyramidal' cell are very characteristic. Such a cell appears in a well prepared vertical section of the cortex as an elongated isosceles triangle placed vertically, with the base looking towards the underlying white substance and the tapering apex pointing to the surface. The cell substance is finely granulated or fibrillated, the fibrillae sweeping round in various directions; it not unfrequently contains pigment. In the midst of this cell-substance rather near the base lies a large clear conspicuous round or oval nucleolated nucleus. At the base the cell-substance is prolonged into a number of processes. One of these, generally starting from about the middle of the base, runs for some distance without dividing, and soon acquiring a medulla may be recognized as an axis cylinder process; the fibre to which it gives origin sweeps with a more or less curved course into the subjacent white matter. In some instances the axis cylinder process, by a T division like that seen in a ganglion of a posterior root (§ 97) gives rise to two fibres, one of which may take a horizontal direction; in some regions of the cortex, the occipital for instance, the axis cylinder process is said to give rise by division to several fibres. The other processes from the base, especially those from the angles of the triangle, rapidly branch into fine fibrils which are soon lost to view in the ground substance. The apex of the triangle is also prolonged into a process, which giving off fine lateral branches, makes as it were straight for the surface, but ultimately branching into fine fibrils is lost to view at some distance from the body of the cell. The cell lies in a cavity of the ground substance which it appears normally to fill, but from the walls of which it sometimes shrinks, developing between itself and the wall of the cavity a space which may contain not only lymph but occasionally leucocytes. In prepared specimens the retraction within its cavity of the artificially shrunken cell may be often observed.

The 'small pyramidal' cells have much the same features; that is to say the cells are characterized by their pyramidal form, though this is naturally not so distinct, by their vertical position, and by the possession of branching processes which are lost in the molecular ground substance; the presence however of a midbasal axis-cylinder process has not been clearly demonstrated.

Other nerve cells are more like the ordinary nerve cells of the spinal cord and of the internal cerebral grey matter; they are branched cells of irregular, not of pyramidal form and for the most part small, 18 μ by 10 μ. They may be characterized by the relative large size (7 μ) of the nucleus, and do not possess an axis cylinder process; at least such a process has not yet been demonstrated. They are frequently spoken of as 'angular' cells.

Another kind of cell, the 'fusiform cell,' which is found in all regions of the cortex has a characteristic spindle shape, the cell-substance being prolonged at the opposite poles into tapering, ultimately branched processes. The long axis of the cell is generally placed horizontally, following the curvature of the cortex, and being thus at the sides of the sulci vertical to the surface of the brain; it is however at times inclined at various angles.

Still another kind of cell, the 'granule cell' or 'nuclear cell,' is one in which the nucleus is surrounded by a relatively small quantity of cell substance, 9 μ by 7 μ, more or less spherical in form in ordinary preparations, but probably breaking up into delicate branched processes. Cells of this kind are sparsely scattered throughout the cortex generally, but in particular regions, e.g. the occipital, are crowded together into a layer, which in many respects resembles the nuclear layer of the cerebellum, and has been called the 'granular' or 'nuclear' layer.

Lastly throughout the cortex are found besides indubitable nerve cells and indubitable neuroglial cells, numerous small somewhat irregular cells, concerning which it may be debated whether they are really nervous or simply neuroglial in nature. Moreover in using the names given above for the various kinds of nerve cells, it must be remembered that many transitional forms are observed; cells for instance may be seen intermediate in form between pyramidal cells and 'fusiform' or 'angular' cells.

The medullated nerve fibres which take part in the cortex may be considered provisionally as forming two categories. In the first place fibres sweep up vertically into the cortex from the subjacent 'central white matter' taking at first a curved course as they enter into the grey matter and then appearing to run straight towards the surface. These are arranged in the deeper levels in bundles, leaving vertical columns of the grey matter between them; but at more superficial levels the bundles spread out and are gradually lost to view. Besides these distinct vertical fibres and bundles of fibres, of the ordinary medullated kind, which we have reason to think are the ends (or beginnings) on the one hand of fibres of the pedal and tegmental systems and on the other hand of fibres of the corpus callosum, or the other commissural fibres spoken of as 'association' fibres (§ 635), an exceedingly large number of fibres of the peculiar fine medullated kind run in various directions forming a dense network in the ground substance of the grey matter between the cells. We may add that this system of fine medullated fibres is of late growth and is not fully developed in man until two or three years after birth. Many of the medullated fibres, coarse as well as fine, take a horizontal direction parallel to the surface, and in certain regions are specially developed into a layer or into two layers so as to form a horizontal streak or streaks.

The vascular pia mater invests closely as we have said the whole surface of the cortex, dipping down into the sulci; and from it, as in the case of the spinal cord, processes carrying blood vessels and bearing lymph spaces pass inwards to supply the grey matter with blood. But while, as we shall see later on, the supply of blood vessels to the grey matter is considerable, the truly connective tissue elements of the pia mater processes are soon merged into neuroglia. Immediately beneath the pia mater forming the immediate surface of the cortex is a thin layer consisting of neuroglia only.

§ 650. The nerve cells of the above several kinds are arranged more or less distinctly in layers parallel to the surface, so that the whole thickness of the cortex may by means of them be, more or less successfully, divided into a series of zones, one above the other; and we may as we have said recognize on the one hand a general arrangement common to the whole surface, and on the other hand modifications existing in the several regions. The general arrangement may be said to be one of five layers or zones, usually counted from the surface inwards.

The fifth layer, lying next to the central white matter, fairly uniform in characters and thickness (about 1 mm.) over the greater part of the brain is characterised by the presence of somewhat sparsely scattered 'fusiform' cells, though other branched cells are present. It is broken up into vertical columns by the bundles of vertical fibres, and its demarcation from the white matter below is somewhat indistinct owing to the fact that in the brain the white matter, especially that lying beneath the cortex, contains cells and small groups of cells lying between the bundles of fibres to a much greater extent than does the white matter of the spinal cord.

The fourth layer, lying above the preceding, varies much more both in thickness (·35 mm. to ·15 mm.) and in its characters. The constituent cells are on the one hand large pyramidal cells, and on the other hand 'granule' or 'nuclear' cells. In some regions it may be subdivided into two layers, the small 'nuclear' cells being so abundant as to form in the upper part of the layer a separate layer called the 'granule' or 'nuclear' layer. This fourth layer like the preceding fifth layer beneath it is split up into vertical columns by the bundles of vertical fibres, but to a less degree. It is marked in its lower part by a horizontal streak due to numerous, mostly fine, medullated fibres running horizontally. In the cortex of the Island of Reil, this horizontal layer is developed into a conspicuous sheet of medullated fibres, separating the fourth and fifth layers by a distinct interval of obvious white matter. This fifth layer, of fusiform cells, thus detached from the rest of the cortex is what is called the *claustrum* (Figs. 115, 116, &c., *cl*).

In the third layer, the constituent cells are the characteristic pyramidal cells. These are for the most part large, though diminishing in size from below upwards, and the layer has been called the "layer of large pyramidal cells," though in certain regions the largest pyramidal cells, and notably the giant cells are found in the preceding, fourth, layer. The cells are on the whole scattered somewhat sparsely, though frequently gathered into small groups, and among them occur small 'nuclear' and other cells. The bundles of vertical fibres spread out rapidly in this layer so that the columnar arrangement becomes lost, and many of the fibres undoubtedly become axis cylinder processes of the pyramidal cells. Though the layer varies in thickness (1 mm. to ·4 mm.) and in some of its features in different regions, the characteristic pyramidal cells are present over the whole surface of the hemisphere. In the lower part of the layer a second horizontal streak of closely interwoven horizontal fibres frequently makes its appearance.

The second layer, generally a thin one, though varying from ·25 mm. to ·75 mm. in thickness, is also formed by pyramidal cells but is distinguished from the layer below by the absence of large and medium sized cells and by the presence of numerous small cells closely packed together; it has been called "the layer of small pyramidal cells." As we have said these smaller pyramidal cells differ somewhat from the larger cells; and the cells in this layer are sometimes described as 'angular.'

The first and most superficial layer is characterized by the predominance of the molecular ground substance, the cells being few, far between, small, and irregular. The ground substance itself seems to be more largely neuroglial in nature than in the other layers, and, as we said above, its extreme surface appears to be furnished by neuroglia alone. The layer is generally spoken of as the 'peripheral' or 'superficial layer,' or sometimes as the 'molecular' layer. The tapering vertical processes of the pyramidal cells may be traced into this layer, which indeed varies in thickness according to the abundance of pyramidal cells in the subjacent layers; numerous somewhat fine medullated fibres also traverse it in a horizontal direction.

§ **651.** The general arrangement just described varies as we have said in different regions of the cerebral surface. We must content ourselves here with pointing out the characteristics of two or three important regions.

The region which we have (§ 632) called the 'motor area' or 'region,' is characterized on the one hand by the great thickness (1 mm.) of the third layer, that of large pyramidal cells, as well as by the number and size of the cells contained in it, and on the other hand and especially, by the prominence in the fourth layer of remarkable clusters of very large pyramidal cells, of the kind which are referred to above, § 649, as being frequently called 'ganglionic'; it is in this region that 'giant cells' are found in the fourth layer, namely, in the upper part of the precentral and at the summit of the postcentral convolution, and in the paracentral lobule, acquiring their greatest size at the top of the precentral convolution.

The occipital region is characterized by the prominence of the 'granule' or 'nuclear' cells. These not only form a distinct division of the fourth layer, but are also conspicuous in other layers, their arrangement being such that some authors have been led to divide the cortex of this region into seven or even eight layers. In the present state of our knowledge we may be content with insisting that the great mark of this occipital region is the abundance of these small 'nuclear' cells together with other small 'angular' cells, whereby the pyramidal cells seem to be made less conspicuous. It is worthy of notice however that in the third, but more especially in the fourth layer, a few cells of very large size are met with, which by their large branched cell substance and conspicuous axis cylinder process resemble the large cells in the motor region; but it should be noted that while these large cells occur, (at least in man and in the monkey, though not in some of the lower animals as the rabbit), in very definite clusters in the motor region, they occur singly in the occipital region. In this occipital region the layer of horizontal fibres in the fourth layer is very conspicuous, and owing to the number of ordinary medullated fibres present forms a white streak visible even to the naked eye.

In the frontal region, in front of the motor region, the arrangement is more in accordance with what we have described as the general plan. The two pyramidal layers are well marked as is also the fourth layer; but the layer of large pyramidal cells is much thinner than in the motor region, as is also, though to a less extent, the fourth layer, while the fifth layer, that of fusiform cells, is thicker than elsewhere. Small 'nuclear' cells are perhaps more abundant in this region throughout all layers than in the motor region, but are far less conspicuous than in the occipital region.

We may here remark that the transition in structure from one region to another is very gradual, not sharp and distinct, and is perhaps especially gradual in passing from the motor region backwards to the occipital region. It is not possible to recognize histologically the limit, for instance, of the motor region as determined experimentally.

In special regions of the brain, for instance in the olfactory bulb of which we shall speak later on, very great modifications of the general plan may be observed in the cortex. We cannot enter upon these but may just refer to the cornu ammonis or hippocampus. At the ventral end of the temporal lobe, the gyrus hippocampi, the structure of whose cortex follows the general plan, is thrust inward so as to project into the cavity of the descending horn of the lateral ventricle, forming the ridge-like prominence known by the above name. The substance of the cornu ammonis is therefore cortical substance covered on the side of the ventricle by a thin prolongation of the central white matter which is in turn covered by the ependyma lining the ventricle. A vertical section of this substance shews that while the fifth and fourth layers are reduced to small dimensions, the third layer, that of large pyramidal cells, is well developed though narrow. The cells are large and remarkably long, and the tapering processes are arranged so regularly as to give rise especially in stained preparations to a marked radiate appearance. At the level of the second layer there occurs a large development of capillary blood vessels and a scarceness of cells, giving rise to a 'lacunar' appearance; and the first or molecular layer is of some considerable thickness. From the prominence of the pyramidal cells in this region, the third layer in the general plan of the cortex has sometimes been spoken of as the "formation of the cornu ammonis."

§ **652.** In the present state of knowledge it is impossible to come to any satisfactory conclusion concerning the meaning of the variety and arrangement of the cells and other constituents of the cortex. The cells with their branches, the nerve fibres and the nerve fibrils form a network of grey matter which we may compare with the grey matter of the spinal cord (§ 579) but which is obviously, as we might expect, far more complex than that is. We may conclude, and experimental observation confirms the conclusion, that the large pyramidal cells with recognisable axis cylinder processes serve as trophic centres for the fibres which appear to start from them. And we may, though with less confidence, explain the large size of these cells in the motor region, by the fact that they give rise to fibres of the pyramidal tract stretching a long way from their origin in the cell, and therefore demanding great nutritive activity on the part of the cell. We may perhaps also conclude that these fibres are efferent, motor fibres, destined to carry impulses from the cortex to peripheral or at least distant parts. And we may further, with however distinctly less confidence, assume that the size of the cell is correlated to the energy which has to be expended in the discharge of efferent, motor impulses. If we accept these conclusions we must also bear in mind, that such cells, with axis cylinder processes continued on as fibres, are not limited to, though most abundant in the motor region, but are found in all regions of the cortex; and we must hence conclude that impulses, which we must call efferent, proceed from all parts of the cortex.

It is obvious however that the connection of the cortical network of grey matter with the fibres of the white matter is effected in part only, and that a small part, by the method of axis-cylinder processes definitely prolonged from the cell substance of cells. A part, and probably a greater part of the fibres sweeping up from the subjacent white matter, whether they be fibres of the pedal and tegmental systems or callosal or 'association' fibres, end in the grey matter in some other way than by bodily being continued into the cell substance of cells; they plunge into and break up within the network, of which fibrils no less than cells form a conspicuous part; and we may here repeat the remark which we made in speaking of the cerebellum concerning the actual continuity of the elements of the network. Moreover, besides the vertical fibres obviously coming from the subjacent white matter, we have in this grey matter to deal with the fibres of horizontal and other directions, which may come from white matter, not far off, but which may come from some neighbouring grey matter; our present knowledge will not enable us to settle this point.

In the spinal cord we were able to divide all the fibres into afferent and efferent respectively; though even here we met with some difficulty. Dealing with the cerebral cortex, which as we have already seen is certainly especially concerned in voluntary movements and in the development of full sensations, we may be tempted to consider the fibres connected with the grey matter as similarly divisible into motor and sensory; and we may go on to suppose that the fibres joining the cortex as axis cylinder processes of recognisable cells are motor fibres, and that all the other fibres joining the grey matter in some other way are sensory fibres. But in doing so we are going beyond our tether; in all probability the nervous processes going on in the cortex are far too complex to permit such a simple classification of the functions of fibres as that into motor and sensory; and any attempt to arrange either fibres or regions of the cortex as simply motor or sensory is probably misleading. But we shall have to return to these matters when we deal with the functions of the cortex.

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SEC. 7. ON VOLUNTARY MOVEMENTS.

§ **653.** When we examine ourselves we recognize certain of our movements as 'voluntary'; we say that we carry them out by an effort of the 'will.' And when we witness the movements of other people or of animals we regard as also voluntary such of those movements as by their characters and by the circumstances of their occurrence seem to be carried out in the same way as our own voluntary movements. Even in the case of some of our own movements we are not always clear whether they are really voluntary or no; and in the case of other people and of animals it is still more difficult to decide the question. It would be out of place to attempt to discuss here how voluntary movements really differ from involuntary movements, or in other words, what is the nature of the will; we must be content to take a somewhat rough use of the words 'voluntary,' 'volitional,' and 'will' as a basis for physiological discussion. We may however remark that as far as the muscular side of the act, if we may use such an expression, is concerned, a voluntary movement does not differ in kind from an involuntary movement. It is perfectly true that a skilled man may by practice learn to execute muscular manœuvres which he would not have learnt to execute had not an intelligent volition been operative within him; but our own experience teaches us that many more or less intricate movements which have undoubtedly been learnt by help of the will may be carried out under circumstances of such a kind that we feel compelled to regard them as, at the time, involuntary; and it may at least be debated whether every movement which we can carry out, by an effort of the will, may not appear under appropriate circumstances as part of an involuntary act. In the case of the lower animals, in the frog deprived of its cerebral hemispheres for instance, we have seen that voluntary differ from involuntary movements, not by their essential nature but by the relation which their occurrence bears to circumstances. We have therefore to seek for the distinction between voluntary and involuntary, not in the coordination of the muscular and nervous components of a movement, but in the nature of the process which starts the whole act.

The histories, related in a preceding section, of various animals deprived of their cerebral hemispheres, while they have further shewn the difficulty of drawing a sharp line between the presence and absence of volition, such as when we appeal to our own consciousness we seem able to draw, have taught us that in a broad sense the presence of volition is, in the higher vertebrata, dependent on the possession of the cerebral hemispheres; and we have now to inquire what we know concerning the way in which the cerebral cortex, for this, as we have seen, is the important part of the cerebral hemisphere, by the help of other parts of the nervous system carries out a voluntary movement.

§ **654**. With this view we may at once turn to the results of experimental interference with the cortex. When the surface of the brain is laid bare by removal of the skull and dura mater, mechanical stimulation of the cortex produces little or no effect, thus affording a contrast with the results of mechanically stimulating other portions of the brain, or other nervous structures. And for a long time the cortex was spoken of as insensible to stimulation. When, however, the electric current is employed, either the make and break of the constant current, or the more manageable interrupted current, very marked results follow. It is found that certain movements follow upon electric stimulation of certain regions or areas. The results, moreover, differ in different animals. It will be convenient to begin with the dog, on which animal the observations of this kind were first conducted.

When the surface of the dog's brain is viewed from the dorsal surface a short but deep sulcus is seen towards the front, running outwards almost at right angles from the great longitudinal fissure; this is called the *crucial sulcus* (Fig. 124), the gyrus or convolution in front and behind it, and sweeping round its end being called the *sigmoid gyrus*. It will hardly be profitable to discuss here either the homology of this sulcus or the names of the other sulci and convolutions of the dog's brain. We mention this sulcus because it is found that stimulation of the cortex in a region which may be broadly described as that of the neighbourhood of this crucial sulcus gives rise to movements of various parts of the body, whereas no such movements result from stimulation of the extreme frontal region in front of the area around the crucial sulcus, or from stimulation of the occipital region behind this area. Certain exceptions may be made to this broad statement, but these it will be best to discuss in reference to the more highly developed monkey.

The region of the cortex in the neighbourhood of the crucial sulcus may then be termed an 'excitable' or 'motor' region, inasmuch as stimulation of this region leads to movements carried out by skeletal muscles, while stimulation of other regions does not. Further, stimulation of particular districts or areas of the region leads to particular movements carried out by particular muscles.

For instance, stimulation of the more median parts of the gyrus behind the crucial sulcus (Fig. 124 ‡‡) leads to movements of the hind limb, whereas stimulation of the lateral part or outer end of the same gyrus leads to movements of the fore limb, and we may here distinguish between an area stimulation of which

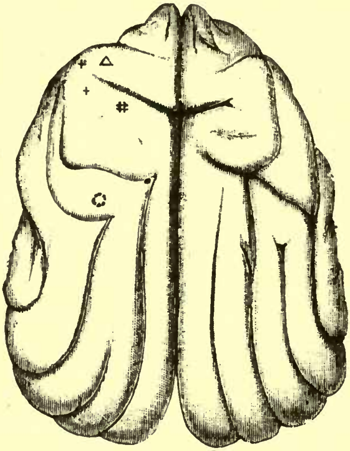

Fig. 124. The Areas of the Cerebral Convolutions of the Dog, according to Hitzig and Fritsch.

(1) Δ The area for the muscles of the neck. (2) ∔ The area for the extension and adduction of the fore limb. (3) + The area for the flexion and rotation of the fore limb. (4) ‡‡ The area for the hind limb. Running transversely towards and separating (1) and (2) from (3) and (4) is seen the *crucial sulcus*. (5) ◌ The facial area.

(Fig. 124 +) leads to flexion of the fore limb, and an area (Fig. 124 ∔) stimulation of which leads to extension of the same limb. In a similar way stimulation of other areas within the ‘motor’ region leads to movements of this kind or of that kind of the tail, of the eyes, of the mouth, of other parts of the face, of the tongue, and so on. Obviously in the dog this region of the cortex has connections with the skeletal muscles which do not obtain between other regions of the cortex and those muscles; and further, the region in question is topographically differentiated, so that certain areas or districts of the region are specially connected with certain skeletal muscles or groups of muscles. We may speak of a ‘localisation of function’ in this region as compared with other regions of the cortex, and in the several areas within the region as compared with each other.

The muscles which are thus thrown into contraction are the muscles of the opposite side of the body. When ‘the fore limb area,’ as we may call it, of the right hemisphere is stimulated, it is the left fore limb which is moved; and so with the other areas;

it is only in exceptional cases, as in certain movements of the eyes, that the effect is bilateral; a movement confined to the same side as that stimulated is never witnessed.

The results are most clear when the current employed as a stimulus is not stronger than is just sufficient to produce the appropriate movement (roughly speaking a current just perceptible to the tongue of the operator is in ordinary cases a useful one), and when the cortex is in good nutritive condition. In any experiment the results obtained by the earlier stimulations, soon after the cortex has been exposed, are the best; after repeated stimulations the surface is apt to become hyperaemic, and it is then frequently observed that the movements resulting from the stimulation of a particular area are not confined to the appropriate muscles, but spread to the corresponding muscles of the opposite side, then to muscles connected with other cortical areas, and at last to the muscles of the body generally; at the same time the movements lose their distinctive purposeful character and the animal is thrown into convulsions of an epileptiform kind. It not unfrequently happens that an experiment has to be stopped in consequence of the onset of these epileptiform convulsions. The response of movement to stimulation may be observed while the animal is under the moderate influence of an anæsthetic, but a too profound anæsthesia lessens or annuls the effects.

In order to carry out a closer analysis of the phenomena it is desirable to watch or record the contraction of a particular group of muscles, or perhaps better still a particular muscle, *e. gr.* the area for extension of the hind limb may be studied by help of the extensor digitorum communis of the limb. When this is done the following important facts may be observed. The area of cortex having been found which gives the best movements, and the stimulus being no stronger than is necessary, isolation of the area from its lateral surroundings by a circular incision carried to some little depth will not prevent the development of contractions in the muscle; but these do cease, even without the circular incision, if by a horizontal section the grey cortex is separated from the subjacent white matter. After removal of the cortex, stimulation of the white matter underlying the area produces the appropriate contraction; not only however is a stronger stimulus necessary, but also the latent period, that is the time intervening between the beginning of the application of the stimulating current and the beginning of the muscular contraction is appreciably shortened. The appropriate contractions not only appear when the white matter immediately below the cortex is stimulated, but by making successive horizontal sections and stimulating each in turn, the effect may, so to speak, be traced through the central white matter of the hemisphere down to the internal capsule. We may conclude from these results, that when the current is applied to the surface of the cortex, certain parts of certain structures in the grey matter are stimulated, the process having a marked latent period, and that as the outcome of the changes induced in the grey matter, impulses pass along the fibres leading down from the grey matter to the internal capsule and so by the pedal system of fibres to the spinal cord and motor spinal roots. The anatomical considerations advanced in a previous section lead us to suppose that the fibres in question belong to the great pyramidal tract, on which we have so much insisted; and as we shall see all our knowledge confirms this view.

It must not, however, be supposed that the several areas stimulation of which produces each its distinctive movement, are in the dog sharply defined from each other; when the term area for extension of the hind limb is used it must not be supposed that the area can be defined by an outline, within which stimulation produces nothing but extension of the hind limb, and outside which stimulation never produces extension of the hind limb. All that is meant is that extension of the hind limb is the salient and striking result of stimulating the area. When we study the various movements, and especially perhaps when we study, by help of a graphic record, the contractions of various individual muscles resulting from the stimulation of various parts of the motor region, we find not only that the areas for particular movements or particular muscles are very diffuse, but that the several areas largely overlap each other. If for instance we were to map out on the same diagram the several areas belonging to four or five muscles of different parts of the body, such as the extensors of the digits of the fore and of the hind limb, the flexors of the same, and the orbicular muscle of the eyelid, that is to say, the several areas within which in turn stimulation of the cortex produced contraction of the particular muscle, the overlapping would be so great that the whole figure would appear highly confused. In a similar way the excitable motor region as a whole would gradually merge into, be broken up into, the unexcitable frontal, occipital and temporal regions, in front, behind and below. In other words, the localisation in the cortex of the dog is to a marked degree imperfect.

In this respect the dog, corresponding to its position in the animal hierarchy, is intermediate between such animals as the rabbit, the bird, and the frog, on the one hand, and the more highly developed monkey on the other; and that is one reason why we have taken the dog first and dwelt so long upon it. In the rabbit, a similar localisation may be observed, but far less definite, far more diffuse; it becomes still less in the bird, and is hardly recognisable in the frog. It will not be profitable to dwell on the details of these lower animals; but the phenomena of the monkey, leading up as they do to those of man, call for special notice.

§ 655. When in a monkey, in an individual for instance belonging to the genus *Macacus*, the surface of the cerebrum is explored with reference to the effects of electric stimulation, it is found that when the current is applied to the precentral or ascending frontal and the post-central or ascending parietal convolutions which lie respectively in front of and behind the important central fissure or fissure of Rolando (cf. Fig. 125), movements of the fore limb follow. The 'motor area for the fore limb' thus discovered is more circumscribed and definite than is the corresponding area in the dog. Its outline (Fig. 126) is roughly that of a truncated triangle bisected by the central fissure, with the broad base at some distance from the mesial line, and the truncated apex reaching on the lateral surface of the hemisphere to a well-marked bend in the lower part of the central fissure. Behind, it reaches as far as the intraparietal fissure which somewhat sharply defines its hind border, and in front it ceases no less definitely at some little distance behind the precentral fissure. Further examination shews that the whole area is divided into areas corresponding to movements of particular parts of the fore arm, and that these are arranged in a definite relation to each other. In the more dorsal part of the area, at the base of the triangle, stimulation produces movements of the shoulder (Fig. 126); if the electrodes be shifted ventrally movements of the elbow make their appearance; if still more ventrally, movements of the wrist come in, and these are in turn succeeded ventrally by movements of the digits generally, of the forefinger, and lastly of the thumb. A very striking experiment may be made by applying a current of suitable strength, first at the lower, ventral border of the area, and then gradually advancing upwards towards the mesial line; the thumb is moved first, then the forefinger, then the rest of the digits, then the wrist, next the elbow, and lastly the shoulder. Further, in certain parts of the area the resulting movement is flexion of the appropriate segment of the limb, in other parts extension, in certain parts abduction, in other parts adduction, and so on.

Similar exploration shews that the "area for the hind limb," lies on the median side of the area for the fore limb, stretching besides on to the mesial surface along the marginal convolution which forms the dorsal portion of the wall of the great longitudinal fissure; it reaches as far back as the intra-parietal sulcus, and is succeeded in front by the "area for the trunk" (Fig. 127). Within this general area for the hind limb we may similarly distinguish special areas for the hip (Figs. 126, 127) in the front portion, for the knee and ankle behind this, and for the digits still farther backwards, the area for the great toe being however in front of the area for the other digits.

In front of the areas for the limbs and trunk, on the median dorsal surface, dipping down into the mesial surface along the marginal convolution (Fig. 127) and reaching laterally on the dorsal lateral surface to the dorsal extremity of the precentral sulcus (Fig. 126), is the "area for the head," that is to say for movements of the head brought about by contractions of the muscles of the neck.

Ventral to this again, in front of the precentral sulcus is the "area for the eyes," that is to say, for contractions of the ocular muscles; and behind the precentral sulcus, ventral to the arm area, lies a small area for movements of the eyelids, brought about by contractions of the orbicularis muscle. Ventral to this again is the 'area for the face,' in which we may distinguish an area for the mouth, that is an area stimulation of which produces changes in the buccal orifice, opening, shutting, drawing to one side &c., and an area for movements of the tongue. These two areas

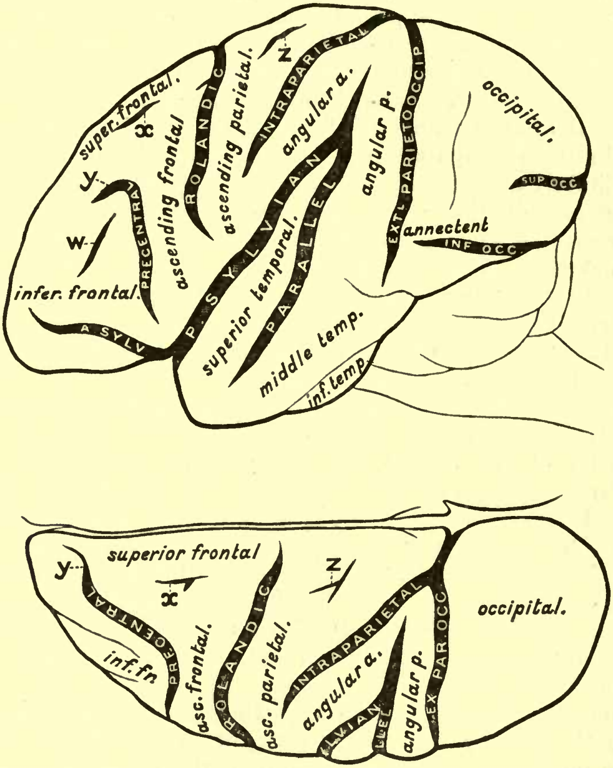
super. frontal.
x
y
w
infer. frontal.
PRECENTRAL
ascending frontal
ROLANDIC
ascending parietal.
INTRAPARIETAL
z
angular a.
angular p.
EXT. PARIETOOCCIP
occipital.
SUP. OCC
annectent
INF. OCC
A. SYLV
P. SYLVIAN
superior temporal.
PARALLEL
middle temp.
inf. temp.
y
superior frontal
x
z
PRECENTRAL
inf. fn.
asc. frontal.
ROLANDIC
asc. parietal.
INTRAPARIETAL
angular a.
SYLVIAN
LLEL
angular p.
EX PAR OCC
occipital.

Fig. 125. Outline of Brain of Monkey (Macacus) to shew principal Sulci (Fissures) and Gyri (Convolutions). (Natural size.) (Sherrington after Horsley and Schäfer.)

The brain figured is the same as that in Fig. 126, and the two figures should be consulted together. Over each sulcus, purposely printed very thick, the name is written in *small capitals*, over each gyrus in *italics*. *x* indicates the small depression, hardly to be called a sulcus, which is supposed to be homologous with the superior frontal sulcus of man; and *w*, *y*, *z* similarly indicate sulci whose homologies are not certain. For some synonyms see Figs. 129, 130.

reach downwards to the fissure of Sylvius, and backwards to the line of the intra-parietal sulcus. In front of them, occupying all the ventral part of the precentral convolution and reaching forwards as far as the precentral sulcus, where it meets the area for the eyes, lies an area stimulation of which produces movements of the pharynx or larynx as well as the mouth or face, and which may be divided into areas for mastication, for swallowing, and for the production of the voice.

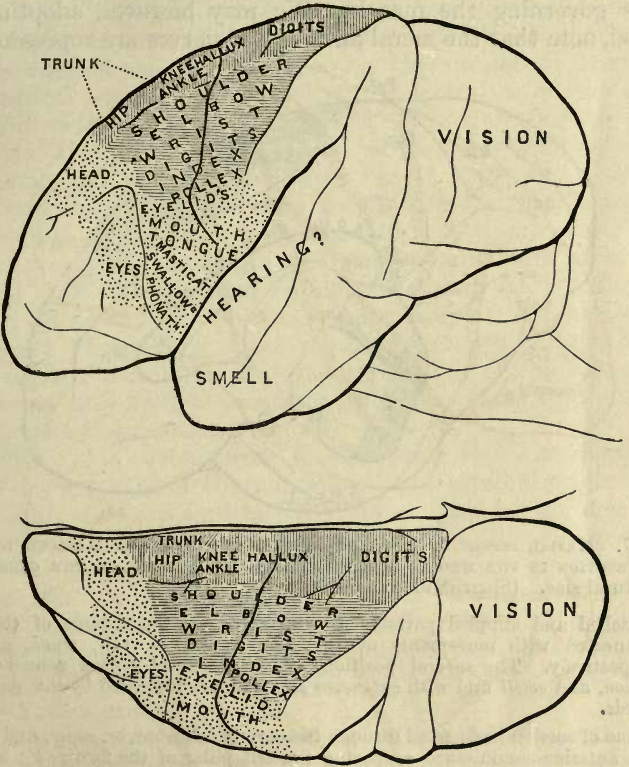
DIGITS
TRUNK
KNEE
HALLUX
ANKLE
HIP
SHOULDER
ELBOW
WRISTS
DIGITS
INDEX
POLLEX
HEAD
EYELIDS
MOUTH
TONGUE
MASTICAT.
SWALLOW
PHONATN.
EYES
HEARING?
VISION
SMELL
TRUNK
HIP
KNEE
ANKLE
HALLUX
DIGITS
HEAD
SHOULDER
ELBOW
WRISTS
DIGITS
INDEX
POLLEX
EYES
EYELID
MOUTH
VISION

Fig. 126. Left hemisphere of the Cerebrum of Macacus Monkey viewed from its left side, and from above. Natural size. (Sherrington after Horsley and Beevor.)

The figure shews the positions of the portions of the cortex concerned with movement of various parts, and with the senses of sight, smell, and hearing. The cortical area connected with the movements of the leg is shaded vertically across, that with the movements of the arm horizontally, and that with the movements of the trunk in a slanting direction; the area connected with movements of the head (neck), face, and eyes is dotted. The course of the chief fissures is indicated by single lines.

We might speak of these several areas in another way by referring to the nerves concerned in carrying out the several movements, though in doing so we must remember that there is not an exact correspondence between the relative position of a muscle along the axis of the body or along the axis of a limb and the relative position along the cerebrospinal axis of the nerve or nerves governing the muscle. We may however, adopting this method, note that the sacral and lumbar nerves are represented by the most mesial portion of the whole motor area and by the hind division of this mesial portion; that the lumbar and thoracic nerves are represented by the front division of the same mesial portion; that the upper thoracic with the lower cervical nerves belong to a region lying lateral to, and the upper cervical nerves to one lying in front of the preceding area; and lastly that the remaining lateral and ventral portions of the whole motor region appertain to the cranial nerves. But the topographical differentiation does

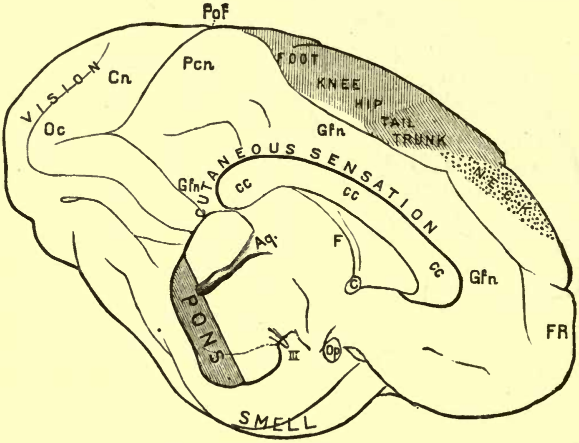

Fig. 127. Mesial aspect of the left half of the Brain of Macacus, displayed by section in the median sagittal plane and removal of the cerebellum. Natural size. (Sherrington after Horsley and Beevor.)

The hatched and stippled parts of the surface shew the regions of the cortex connected with movements of the *foot*, *knee*, *hip*, *tail*, *trunk*, and *neck* respectively. The several positions of the areas of cortex connected with *vision*, and *smell* and with *cutaneous sensation* are indicated by the appropriate words.

The plane of section has passed through the corpus callosum, *cc*, *cc*, *cc*, and through the anterior commissure, *c*, sparing the left pillar of the fornix, *F*; behind it has bisected the anterior part of the pons, laying open the aqueduct, *Aq.* (iter a tertio ad quartum ventriculum). *Pons*, the left half of the pons in frontal section. *Op.* the optic commissure cut across.

III. the root of the third cranial nerve.

FR. the frontal pole, *OC.* the occipital pole; *Cn.* the cuneus, *Pcn.* the precuneus; *G. fn. G. fn. G. fn.* the gyrus fornicatus; the unlettered fissure seen to form the upper boundary of this gyrus in its supra-callosal part is the calloso-marginal, *Po. f.* the parieto-occipital fissure.

not come out so clearly by this method, as by that of taking for our guide distinctive movements of the several parts of the body.

It will be observed that all these areas taken together, represented by the portion of Figs. 126, 127 shaded in one way or another, occupy chiefly the parietal region of the cerebral surface though they also reach into the frontal region. Stimulation of the frontal region in front of this motor area or of the occipital region behind, whether on the lateral or on the mesial surface, or of the temporal region, whether also on the lateral or on the mesial surface, or of the gyrus fornicatus (Fig. 127) connecting the frontal and occipital regions on the mesial surface, and running ventral to the marginal gyrus, does not give rise to movements; or to be more exact, does not give rise to movements comparable to those just described as resulting from stimulation of various parts of the motor region. Movements do take place when certain parts of the occipital or of the temporal region are stimulated, but these are not only feeble and experimentally uncertain, but appear to be of a different nature from those resulting from stimulation of the motor region; it will be convenient to speak of the nature and meaning of this kind of movement when we come to discuss the development of sensations.

§ **656.** It is obvious from the foregoing that the mechanism for the development of these movements of cerebral origin are far more highly differentiated in the monkey than in the dog. But even in the monkey (Macacus and allied forms) the differentiation is still very incomplete. If we explore for instance the area for the wrist we find that its limits are ill-defined. In some parts of the area we obtain movements of the wrist only, but in other parts of the area stimulation produces not only movements of the wrist, but also of the shoulder or of the digits, or of the neck; and so with the other areas.

If, however, not a Macacus or other ordinary monkey, but the more highly developed ourang otang be taken as the subject of experiments, the differentiation is found to be distinctly advanced; the several areas are more sharply defined, and what is important to note, the respective areas tend to be separated from each by portions of cortex, stimulation of which gives rise to no movement at all.

The opportunities of stimulating the cortex of man himself have been few and far between, and have for the most part been conducted under unfavourable circumstances; but as far as the results so obtained go, they shew that the topographical distribution of areas for the several movements is carried out on the same plan as in the monkey (we are purposely confining ourselves now to the results of artificial stimulation); and moreover, justify the conclusion, which *a priori* reasons would lead us to adopt, that in man the differentiation is advanced still farther than in the monkey.

Thus when we survey a series of brains in succession, from the more lowly frog, through the bird, the rabbit, the dog, and other lower mammals up to the monkey, the anthropoid ape, and so to man himself, we find an increasing differentiation of the cerebral cortex, by which certain areas of the cortex are brought into special connection with certain skeletal or other muscles in such a way that stimulation of a particular portion of the grey matter gives rise to a particular movement and to that alone.

§ **657.** In treating of the structure of the brain we spoke (§ 632) of the pyramidal tract as starting from the motor region of the cortex; and it is obvious that the fibres of this tract must be concerned in the development of the movements which we have just described. When the movements are brought about by stimulation of the fibres in some part of their course, in the internal capsule for instance, there can be no doubt that the stimulation starts impulses which, travelling down the tract to the origins of certain cranial or spinal nerves, in some way give rise to coordinate motor impulses along the motor fibres of the nerves; and we may with reason speak of the impulses then passing along the tract as motor or efferent in nature. When the stimulus is applied direct to the cortex, we may assume that processes, started in the grey matter, eventuate in similar efferent impulses along the fibres of the tract. All the evidence leads us to regard this tract as an efferent tract.

When the spinal cord is divided in the lower dorsal region and the electrodes of an electrometer are brought into connection with the transverse cut surface and with some point of the longitudinal surface above, the electrometer gives evidence of currents of action (manifested as negative variations of a demarcation current or current of rest, § 67) whenever the motor area of the hind limb is stimulated, but not when other parts of the cortex are stimulated. We have already said that stimulation of any part of the motor region may under abnormal conditions give rise to general epileptiform convulsions; when these occur during such an experiment as the above, currents of action manifest themselves in the lower dorsal cord, whether the stimulation giving rise to the convulsions be applied to the area for the hind limb or to any part of the motor region. It has been further observed that the currents of action developed within the spinal cord tally in a very exact manner with the muscular movements. The convulsions begin with a sustained 'tonic' contraction of the muscles, and the electrometer shews a similar sustained current of action; this is followed by rhythmic movements of the muscles, accompanied by corresponding rhythmic movements of the mercury of the electrometer. Without insisting too much on the exact interpretation of these results we may take them as at least shewing that, when the motor region of the cortex is excited, nervous impulses accompanied by "currents of action" pass downward along the fibres of the pyramidal tract.

The results of stimulating the fibres of the tract in their course through the corona radiata and the internal capsule, and the results obtained by studying the degenerations following upon injury to or removal of the several parts of the cortical motor region, agree in marking out the paths taken by the several constituents of the tract through the central white matter of the hemisphere, the corona radiata and the capsule. Comparing Figs. 126, 127 with Figs. 121, 122 and 123 it will be seen that the portion of the tract destined for the cranial nerves, and so for the movements of the eyes, the mouth, face, tongue, pharynx and larynx, starting from the ventral parts of the more frontal district of the motor region, take up their position at the knee of the internal capsule; and the portion destined for those upper cervical nerves which carry out movements of the head through the muscles of the neck, starting from the extreme frontal and dorsal parts of the area, is also apparently directed to the knee of the capsule. The rest of the tract, starting from the part of the area lying at once behind and mesial to the above, occupies in the capsule a position posterior to them in the hind limb of the capsule; and it will be observed that the tract for the fore limb which begins on the surface lateral of the tracts for the trunk and hind limb, shifts its course in relation to theirs, so that in the capsule it is in front of them, not lateral to them. It may further be observed that while in the tracts for the trunk and hind limb the same fore and aft order which obtains on the surface is reproduced in the capsule, even apparently to the strange precedence of the ankle over the knee, the order of the several elements in the fore limb tract which is lateral on the surface becomes regularly fore and aft in the capsule. In the capsule the several elements are arranged in a linear order, corresponding broadly to that of the distribution of the muscles along the longitudinal axis of the body; on the cortex they are disposed in an order the cause of which is at present not very clear, but which is probably determined by the respective relations of the several parts of the motor region to the functional activity of the other parts of the cortex. In the shifting from the one order to the other, the several constituent fibres, as we have said, describe a somewhat peculiar course; and when we remember, as stated in § 632, that the order shewn in Fig. 121 is only the order obtaining at one particular level of the capsule, and that from the dorsal beginnings of the capsule in the corona radiata to its ventral end in the pes, the capsule is continually changing in form, and its fibres therefore continually shifting their relations to each other, the whole course of the several fibres of the tract from their origin in the cortex until they are gathered up into the central portion of the pes (Fig. 114 *Py*) must be a very complicated one.

When the area of one hemisphere is stimulated, the movement which results is in most cases seen on the other side of the body, and on that other side alone. Thus when the area for the fore limb is stimulated on the left hemisphere it is the right fore limb which is moved. This is in accordance with what we have learnt of the pyramidal tract and its ultimate entire decussation before it reaches the motor nerves, the decussation either occurring massively as in the case of the crossed pyramidal tract, or in a more scattered manner along the upper part of the spinal cord in the case of the direct pyramidal tract; and, as we have seen, there is a similar decussation for such part of the pyramidal tract as is connected with the cranial nerves above the decussation of the pyramids. Except in the case of certain areas for movements naturally bilateral of which we shall speak presently, the movement is normally on the crossed side, and on the crossed side only. Under abnormal conditions however the limb of the other side, that is of the same side as the hemisphere stimulated, may move also. But such an abnormal movement of the same side has not the same characters as the proper movement of the crossed limb. Instead of being an orderly coordinate movement, it is a more simple, either tetanic or perhaps tonic, or rhythmic, clonic, contraction of the muscles. Obviously its mechanism is of a different nature from that by which the proper movement of the crossed limb is effected; but it is important to bear in mind that a movement of the uncrossed limb may take place; and further that, the abnormal conditions continuing, similar movements of an uncoordinated character may spread to the hind limb and other parts of the crossed side, though the stimulation be still confined to the arm area, then to other parts of the uncrossed side, until as we have said the whole body is thrown into epileptiform convulsions. This feature must not be forgotten. It fact it may be fairly insisted upon that while we may speak of a particular coordinate movement as being the normal outcome of an ordinary careful stimulation of a particular area in a normal condition, it is no less true that diffuse uncoordinated movements, culminating in general epileptiform convulsions, are the natural outcome of the stimulation of any area in an abnormal condition. And in attempting to form any opinion of the nature of the first act, we must bear the second in mind.

As we said above, the movements resulting from cortical stimulation are most conveniently described in terms of parts of the body, of the arm, of the thumb, of the tongue, &c. The movements of the same part may be further distinguished by means of the nomenclature usually adopted in speaking of muscular movements, such as flexion, extension, abduction, adduction, &c.; so that, within the area bearing the name of some particular part, such as the wrist for instance, we have to distinguish an area for the flexion, and another for the extension of that joint; and in like manner in reference to other parts. But it will be readily understood that it is easier to map out the area for a particular part than to distinguish the areas corresponding to the several movements of that part. Hence the nomenclature usually adopted in speaking of the motor region is one based on the parts of the body moved rather than on the character of the movements. The more closely however the movements in question are studied, the more probable it appears that the localisation which obtains in the cortex is essentially a localisation corresponding not to parts of the body, or to nerves, or to muscles, but to movements. In considering this point it must be remembered how rude and barbarous a method of stimulation is that of applying electrodes to the surface of the grey matter compared with the natural stimulation which takes place during cerebral action; the one probably is about as much alike the other, as is striking the keys of a piano at a distance with a broomstick to the execution of a skilled musician. Were it in our power to stimulate the cortex in any way at all approaching the natural method, we should in all probability arrive at two results; on the one hand we should be able to produce at will a variety of movements of different degrees of complexity, some very simple, others very complex, and for these we should have to use names suggested by the characters and purpose of each movement, and by these alone; on the other hand we should find very decided limits to the number and kind of movements which we could evoke, limits fixed in the case of each subject partly by inherited organisation, partly by the training of the individual.

Some such results of refined experimentation are indeed already foreshadowed by the rude results of our present rough methods. The movements which usually follow stimulation of the motor region, and which we have described as flexion, &c., are, so to speak, the elementary factors of ordinary bodily movements the detached and imperfect chords of a musical piece; and in the following facts relating to their production we can recognize the influences of organisation and habit. As we have said, stimulation of the motor area of one hemisphere produces movements, as a rule, which are limited to one side of the body, and that the opposite side. Now both in ourselves and in the higher animals a large number of bodily movements, especially of the limbs, are habitually unilateral; and, putting aside the question why there should be two halves of the brain, and why the one half of the brain should be associated with the cross half of the bodily, we may recognize in the unilateral crossed movement resulting from stimulation of the cortex an accordance with natural habits. But some movements of the body are ordinarily bilateral; the two eyes, for instance, are ordinarily moved together, and the two sides of the trunk move together very much more frequently than do the two fore limbs or the two hind limbs. And in accordance with this we find that stimulation of the motor area for the eyes on either hemisphere produces movements of both eyes, and stimulation of the trunk area of one hemisphere is also very apt to produce bilateral action of the trunk muscles; in such instances the movements on both sides are quite normal movements. We may incidentally remark that removal of the trunk area leads to a good deal of bilateral degeneration, that is, to degeneration of strands in the pyramidal tracts of both sides, whereas such a bilateral degeneration is comparatively scanty after removal of the leg or arm area.

That it is the movement and not the part moved which is, so to speak, represented on the cortex is further shewn by the relative magnitudes of the several cortical areas when they are mapped out according to parts of the body. The area for the arm, for instance, cf. Figs. 126, 127, is, so to speak, enormous compared to that of the trunk when the relative bulks of these two parts of the body are considered; and within the arm area itself the space occupied by the thumb and fore-finger and digits is, bulk for bulk, out of proportion to the space allotted to the shoulder; so also the area for the eyes or for the mouth is out of proportion to the size of those organs. But these relative sizes of the respective areas become intelligible when we bear in mind relative mobility, nimbleness and delicacy of execution; in these respects the shoulder is far behind the thumb, while the eyes and mouth surpass most other parts of the body.

We are brought yet a step further when we compare, in respect of the cortical motor region, animals of different grades of organisation; and the results thus obtained lead us to the conclusion that the motor region is correlated not to movements in general, but to movements of a particular kind. Taking in series the rabbit, the dog, the monkey and man, we find in passing from one to the other, an increase in prominence and in differentiation of the motor region accompanied by an increase in the bulk of the pyramidal tract; among the many striking differences between the brains of these several animals, these two features, the increasing complexity of the motor region, and the increasing size of the pyramidal tract, are among the most striking. The size of the pyramidal tract is itself correlated to the complexity of the motor region, and, being the more easily determined, may be used as indicating both; the difference in the size of the pyramidal tract in these animals is seen all along the whole length of the cord (Fig. 128). Now as regards mere quantity of movement, if we may use such an expression, the differences between these animals are of no great moment. If we were to take the amount of energy expended as movement in twenty-four hours per gramme of muscle present in the body in each of the four cases, we should certainly not find any correspondence between that and the size of the pyramidal tract. If however we take a particular kind of movement, what we may perhaps call skilled movement, that is movement carried out by means of intricate changes in the central nervous system, we do find a remarkable parallelism in the above cases between the amount of such skilled movement entering into the daily life of the individual and the size of the pyramidal tract. In these two respects man is much above the monkey, and the monkey far above the dog. We may conclude then that the cortical motor region is in some way especially concerned with the kind of movement which we have called 'skilled.'

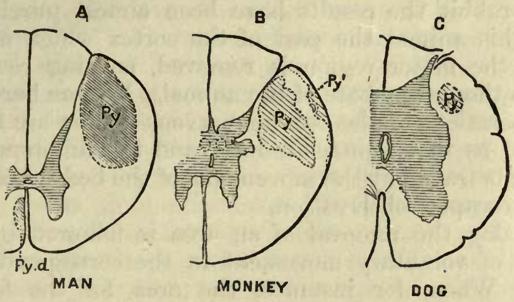

FIG. 128. DIAGRAM TO ILLUSTRATE THE RELATIVE SIZE OF THE PYRAMIDAL TRACT IN THE DOG, MONKEY AND MAN. (Sherrington.)

The figure shews in outline the lateral half of the cord, at the level of the fifth thoracic nerve, in *A*. Man, *B*. Monkey, *C*. Dog; *A* is a reproduction of D^5 in Fig. 104; *B* and *C* are drawn of the same size as *A*. *Py*., shaded obliquely, the pyramidal tract; the depth of shading indicates that the tract is more crowded with true pyramidal fibres as well as larger in *A* than in *B*, and in *B* than in *C*. In *B*, *Py'* is an outlying portion of the pyramidal tract separated from the rest by the cerebellar tract. *Py.d.* the direct pyramidal tract, present in man only. The grey matter seems relatively large in *C* because the section was taken from a very young puppy.

§ 658. These skilled movements are to a large extent, though not exclusively, voluntary movements. We have in a previous section seen reason to believe that the cerebral cortex is in some way especially associated with the development of voluntary movements. Putting together this conclusion and the conclusions just arrived at we are naturally led to the further conclusion that the cortical motor region, with the pyramidal tract belonging to it, plays an important part in carrying out voluntary movements. Do other facts support this view, and if so, what light do they throw on the question as to what part and what kind of part the motor region thus plays?

In this connection we naturally desire to know what are the results of removing from an otherwise intact animal the whole motor region, and more especially this or that particular portion of it. Before proceeding further, however, we may once more call attention to the caution given in § 582, and repeated in § 640; indeed when we consider the high organisation and complex functions which obviously belong to the cortex, when we bear in mind that it appears to govern, and must therefore be bound by close ties to almost all the rest of the central nervous system, we must be prepared to find after removing a portion of cortex that the pure 'deficiency' phenomena, those which result from the mere absence of a piece of the cortex, are largely obscured by the other effects of the operation.

In the rabbit the results have been almost purely negative. When in this animal the part of the cortex which may be considered as the motor region is removed, nothing remarkable is observed in the movements of the animal. We can hardly suppose that the operations of the central nervous system are the same in an operated as in an intact animal, and the differences induced ought to be betrayed by the movements of the body; but at present they have escaped observation.

In the dog the removal of an area is followed by a loss or diminution of voluntary movement in the corresponding part of the body. When, for instance, the area for the fore limb is removed from the left hemisphere, the right fore limb is completely or partially 'paralysed.' In carrying out its ordinary movements the operated animal makes little or no use of its right fore limb. But this state of things is temporary only. After a while the animal regains power over the limb, and in successful cases recovery is so complete that it is impossible to point out in the limb any appreciable deviation from the normal use. And careful examination after death has shewn not only that the area had been wholly removed, but also that there was no regeneration of the lost parts; the removal of the cortex leads in such cases, as usual, to degeneration of the corresponding strand in the pyramidal tract right away from the cerebral surface to the endings of the strand in the cervical and dorsal spinal cord. Nor can it be urged in such cases that diffused remnants of the arm area had been left in the remaining parts of the motor region; for the whole motor region has been removed, and yet the animal has recovered to such an extent that a casual observer could detect no differences between the movements of the two sides of the body. Closer examination did disclose certain imperfections of movement; but the operation had involved injury to or produced changes in structures other than the motor region, and the imperfections might have been due to the additional damage. Nor can it be urged that, in such a case, where one side is removed, the remaining hemisphere takes on double functions; for the greater part of the motor areas have been removed on both sides, and yet the animal's movements have been so far apparently complete that a casual observer would see nothing strange in them. Again, the whole motor region has been removed from one hemisphere in a young puppy, and some time later when the movements seemed to have recovered their normal condition, the removal of the motor region of the other hemisphere has produced merely a paralysis of the crossed side of the body, and that as before only of a temporary character.

Two things have to be noted here. In the first place the removal of an area does affect the movements which are brought about by stimulating that area, it leads to their disappearance or at least to great diminution of them; and this affords an additional argument that the connection between the area and the movement is a real and important one. In the second place, the physiological effect is temporary only, though the anatomical results of the operation are permanent, for the cortex is never renewed, and the pyramidal tract degenerates along its whole length, never to be restored; this shews that we have to deal here with events of a very complex character. When a particular movement results from stimulation of the appropriate cortical area, we may be sure that whatever takes place in the cortex and along the pyramidal tract, motor impulses, duly coordinated, pass along certain anterior roots to certain muscles; and we know that if we removed a sufficient length of each of those anterior roots that particular movement would be lost for the rest of the life of the individual. We may therefore infer that the events which, whatever be their exact nature, taking place in the cortex and along the pyramidal tract lead ultimately to the issue of motor impulses along the anterior roots, differ essentially from the events attending the transmission of ordinary motor impulses.

In the case of the monkey, the results of removing parts of the cortical motor region have not been so accordant as in the case of the dog. The two animals agree perfectly in so far that the removal of a particular area leads, as an immediate result, to the loss of the corresponding movement; but while in some instances recovery of the movement has in the monkey as in the dog after a while taken place, in other instances the 'paralysis' has appeared to be permanent. As a rule the paralysis caused by a large lesion is not only more extensive, but also of longer duration than that caused by a small one; and natural bilateral movements, as of the eyes, reappear earlier than unilateral movements. The facts however within our knowledge relating to the permanence of the effect are neither numerous nor exact enough to justify at present a definite conclusion. On the one hand the positive cases where recovery has taken place are of more value than the negative ones, since in the latter the recovery may have been hindered by concomitant events of a nature which we may call accidental; and it is at least a priori most unlikely that the pyramidal tract mechanism, if we may use the expression, though it may differ in the monkey and the dog in degree of development, differs so essentially in kind that damage of it leads in the one case to permanent, and in the other to mere temporary loss of function. We may add that we should further expect to meet in the monkey with more prominent and more lasting complications due to the subsidiary effects of the operation, and it may be doubted whether in any of the recorded experiments the animal has been allowed to live a sufficient time for these subsidiary events to have cleared away, leaving only what we have called the 'deficiency' phenomena, due to the loss of the cortical area alone. On the other hand it must be remembered that the movements of the monkey are more intricate in origin, more 'skilled' than those of the dog; and it may be that differences in the characters of movements determine the possibility of their recovery. In illustration of this we may quote the experience that, after the removal of the arm area in the monkey, a certain awkwardness in the movements of the thumb is one of the last effects of the operation.

§ 659. Before we proceed however any further in the discussion, it will be of advantage to turn aside to what is known concerning the cortical motor region in man. As we have already said, theoretical considerations lead us to believe that the cortical motor region in man is disposed in accordance with the plan of the anthropoid ape as ascertained experimentally, but with the differentiation carried still further; and the few cases of experimental stimulation of the human cortex support this view. Our chief knowledge in this matter is derived from the study of disease; and in this, the advantages of dealing with one of ourselves are largely counterbalanced by the disadvantages due to disease being so often anatomically diffuse and physiologically changeful and progressive.

We said above that during experiments on animals stimulation of any part of the motor region may under abnormal conditions lead to general epileptiform convulsions. Now clinical study has shewn that in man certain kinds of epileptic attacks are of similar cortical origin. In these cases it has been observed that the attack begins in a particular movement, by contractions of particular muscles, or of the muscles of a particular region of the body, of the hand, foot, toe, thumb, &c., and then spreads in a definite order or 'march' over the muscles of other regions until the whole body is involved. When in an experiment on an animal epileptiform convulsions supervene, they similarly start from the region of the body, the motor area of which is beneath the electrodes at the time, and similarly spread by a definite 'march' over the whole body. Hence in the human epileptiform attacks of which we are speaking, it has been inferred that the immediate exciting cause of the attack is to be sought in events taking place in that part of the cortex which serves as the area for the movement which ushers in the attack. Further inquiry has not only confirmed this view, but has also shewn that the topography of the cortical areas in man, as thus determined, very closely follows that of the monkey.

Other diseases of the cortex have been marked, among other symptoms, by loss or impairment of particular movements. In most of such cases, the cortical lesion has been of such an extent as to involve a number of special areas at the same time, and so to lead to loss or impairment of movement over relatively considerable regions of the body, such as the whole of one arm; and in general the teaching of these cases of disease, while confirming the deductions from the monkey, and giving us some general idea of the topography of the human motor cortical region, has at present given us approximate results only. Figs. 131 and 132 shew in broad diagrammatic manner the position and relative extent of the motor areas for the leg, arm and face in man, as far as has yet been ascertained. To assist the reader we give at the same time diagrams Figs. 129, 130 illustrating the nomenclature of the surface of the human brain.

One area is of special and instructive interest. Speech is an eminently 'skilled' movement. We have seen that in the monkey the area for the mouth and tongue lies at the ventral end of the central fissure or fissure of Rolando, ventral to the arm area, and that the extreme ventral and front part of the motor region just above the fissure of Sylvius supplies an area which we marked as that of phonation (Fig. 126). In the monkey the area of phonation is determined by experimental stimulation; in man, in a similar position, on the third or lowest frontal convolution, sometimes called Broca's convolution, ventral to and in front of, and probably overlapping backwards the area which in Fig. 131 is marked 'face' and which includes the mouth and tongue, clinical study has disclosed the existence of an area which may be spoken of as the area of 'speech.' Lesions of the cortex in this area cause a loss of or interference with speech, the condition being known as *aphasia;* to this we shall presently return. In Fig. 131 this area is shewn in an approximate manner.

The movements of speech are essentially bilateral movements. In the dog and monkey various bilateral movements may be excited by stimulation of the appropriate area in either hemisphere; and analogy would lead us to suppose that in man, the movements of speech would be connected with the speech area in both one and the other hemisphere. The results of lesions however shew that it is in most cases especially the left hemisphere which is connected with speech; it is a lesion in the third frontal convolution of the left hemisphere, often associated with other lesions of the same hemisphere leading to paralysis of the right side of the body and face, which causes aphasia, it being only in exceptional cases that the condition results from a lesion of the corresponding area of cortex on the right hemisphere.

In man, then, clinical study corroborates the conclusions deduced from the experimental investigation of the dog and of the monkey, but still leaves us in uncertainty as to the question what,

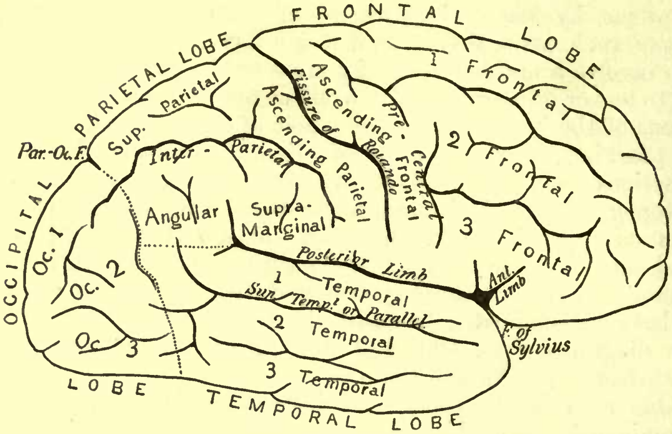
FRONTAL LOBE
PARIETAL LOBE
OCCIPITAL LOBE
TEMPORAL LOBE
Par.-Oc. F.
Sup. Parietal
Inter-Parietal
Ascending Parietal
Fissure of Rolando
Ascending Pre-Central Frontal
1 Frontal
2 Frontal
3 Frontal
Angular
Supra-Marginal
Oc. 1
Oc. 2
Oc. 3
Posterior Limb
Ant. Limb
F. of Sylvius
1 Temporal
Sup. Temp.l or Parallel
2 Temporal
3 Temporal

FIG. 129. DIAGRAM OF THE GYRI (CONVOLUTIONS) SULCI, (FISSURES) ON THE LATERAL SURFACE OF THE RIGHT HEMISPHERE OF MAN. (Gowers.)

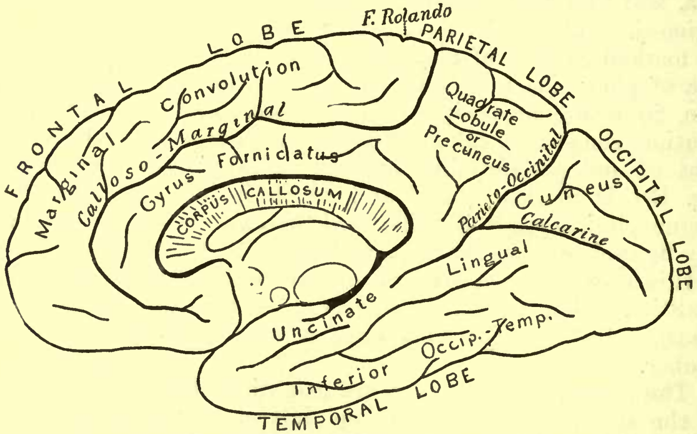
F. Rolando
FRONTAL LOBE
PARIETAL LOBE
OCCIPITAL LOBE
TEMPORAL LOBE
Marginal Convolution
Calloso-Marginal
Gyrus Fornicatus
CORPUS CALLOSUM
Quadrate Lobule or Precuneus
Parieto-Occipital
Cuneus
Calcarine
Lingual
Uncinate
Occip.-Temp.
Inferior

FIG. 130. THE SAME ON THE MESIAL SURFACE. (Gowers.)

In both figures the sulci are indicated by italic and the convolutions by roman type.

The following list of some synonyms may perhaps be of use in connection with these figures and those of the brain of the monkey Figs. 126, 127.

Gyri, or Convolutions. Precentral or anterior central = ascending frontal. Postcentral or posterior central = ascending parietal. Superior temporal = inframarginal = first temporal. Triangular lobule = cuneus. Central lobe = Island of Reil. Paracentral lobule = the mesial face of the superior frontal, within the marginal gyrus. Cingulum = the part of the gyrus fornicatus which adjoins the Corpus callosum. Gyrus Hippocampi = uncinate gyrus, though the latter name is sometimes restricted to the front part of the hippocampal gyrus; the two may be considered as a continuation of the gyrus fornicatus, and the three together, forming a series, have been called "the great limbic lobe."

Sulci or Fissures. Central = Rolandic, or of Rolando. Perpendicular = parieto-occipital. Parietal = intraparietal or sometimes interparietal.

Temporo-sphenoidal lobe = temporal lobe.

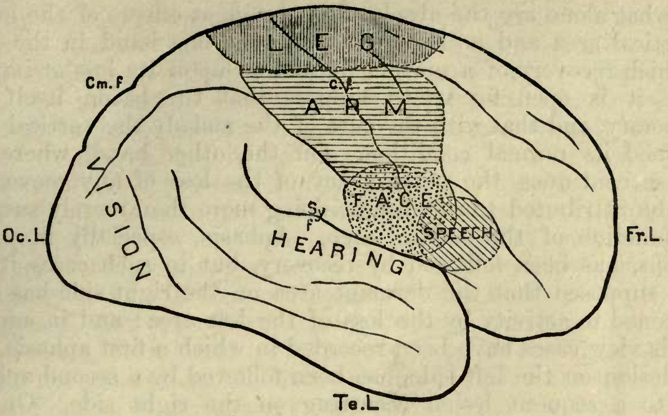

FIG. 131. THE LATERAL SURFACE OF THE RIGHT CEREBRAL HEMISPHERE OF MAN IN OUTLINE, TO ILLUSTRATE THE CORTICAL AREAS. Reduced from nature.

The position of the areas of the cortex concerned with movements of the face, arm, and leg, and with the senses of sight and hearing are approximately shewn. The position of the area connected with speech (Broca's centre) is also shewn for the sake of comparison of it with the position of the other areas; the representation of speech in the cortex cerebri lies however in the *left* hemisphere chiefly.

Oc. L. Occipital lobe; *Fr. L.* Frontal lobe; *Te. L.* Temporal lobe; *Sy. f.* the fissure of Sylvius; *C. f.* the central fissure (Rolandic); *Cm. f.* indicates the position of the posterior end of the calloso-marginal fissure.

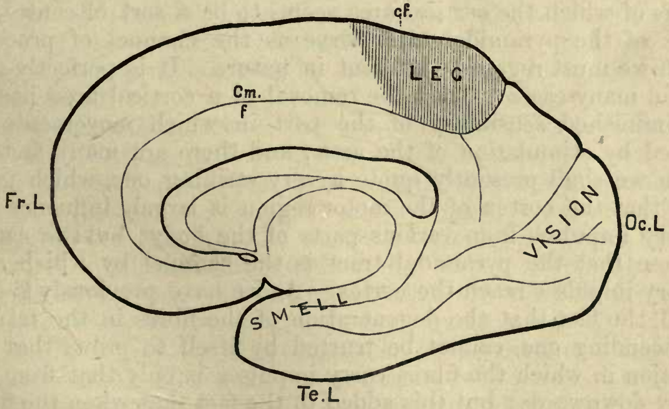

FIG. 132. THE MESIAL SURFACE OF THE RIGHT CEREBRAL HEMISPHERE OF MAN IN OUTLINE, TO ILLUSTRATE THE CORTICAL AREAS.

The areas shown are those connected with the movements of the leg, and with the senses of sight and smell.

Fr. L. the frontal pole of the hemisphere; *Oc. L.* the occipital pole, *Te. L.* the temporal pole. *Cm. f.* the calloso-marginal fissure separating the marginal gyrus above from the gyrus fornicatus below. *Cf.* marks the situation of the central fissure, the fissure itself not being apparent on the mesial aspect of the hemisphere. The corpus callosum and the anterior commissure are seen in cross section.

and what alone are the absolutely permanent effects of the loss of a cortical area and nothing else. On the one hand, in the cases in which recovery of a movement follows upon its loss or impairment, it is open for us to suppose that the lesion itself was temporary, and that with the cure of the malady the cortical area regained its normal condition. On the other hand, where the disease continues, the permanency of the loss of any movement may be attributed to the disease doing more than merely suspend the function of the cortical area. Aphasia, especially in young persons, has been followed by recovery, but in such cases it has been supposed that the dormant area on the right side has been awakened to activity by the loss of the left area; and in support of this view cases have been recorded in which a first aphasia, due to a lesion on the left side, has been followed by a second aphasia due to a sequent lesion occurring on the right side. On the whole perhaps the evidence of clinical study tends to shew that in man the loss of movement due to the destruction by disease of an area is a permanent one, though actual demonstration of this is wanting.

§ **660**. We may now return to the discussion of the question, what is the part played by a motor area, and by the contribution from that area to the pyramidal tract in carrying out the movements with which the area is associated?

We may premise that the evidence points very distinctly to the conclusion that whatever be the nature of the whole chain of events of which the cortical area seems to be a sort of centre, the fibres of the pyramidal tract serve as the channel of processes which we must regard as efferent in nature. It is perfectly true that in many cases at least the removal of a cortical area has led to diminished sensibility of the part in which movements are excited by stimulation of the area; and there are many facts, of which we shall presently quote a very striking one, which go to shew that the cortex of the motor region is largely influenced by sensory impulses from various parts of the body; but we cannot suppose that the pyramidal tract is the channel by which such sensory impulses reach the cortex. As we have previously (§ 568) urged, the fact that the degeneration of the fibres in the tract is a descending one, cannot be trusted by itself to prove that the direction in which the fibres carry impulses is only that from the cortex downwards; but this added to the fact that when the fibres of the tract are stimulated at any part of their course, movements, the signs of the occurrence of efferent centrifugal impulses, are produced, leaves no doubt that the tract is one of efferent fibres. Hence we may infer that whatever be the nature of the events taking place in a motor area during the carrying out of a movement, the part played by the fibres of the pyramidal tract is that of carrying efferent impulses from the area to the muscles concerned.

Let us consider first the movements of speech in man, the evidence touching the connection of which with an area on the third frontal convolution appears so very clear. Speech is eminently a 'skilled' movement; it involves the most delicate coordination of several muscular contractions, and we may certainly say of it that it has to be 'learnt.' The whole chain of coordinated events by which the utterance of a sentence, a word, or any vocal sign is accomplished consists of many links, the breaking of any of which will lead to failure of one kind or another in the act. Something may go wrong in the glossal or other muscles, in the nerve endings in those muscles, or in the fibres of the nerves, hypoglossal and others, between the central nervous system and the muscles, or something may go wrong in that part of the central nervous system, the bulb to wit, in which a certain amount of coordination is carried out just previous to the issue of the motor impulses. Damage done to any of these parts of the mechanism may lead to dumbness or to imperfect speech. In the latter case the imperfections have a certain character; if we are at all able to gather the wish of the speaker, we recognize that he is attempting to utter the right words in the right sequence, but that his efforts are frustrated by imperfect coordination or imperfect muscular action; his speech is 'thick', the syllables are blurred and the like. Disease of the bulb at times leads to imperfect speech of this kind in which the imperfection may be recognized as due to the lack of proper coordination of motor impulses. The affection of speech, known as 'aphasia,' which is caused by lesions of the cortex is of a different character, and the forms of imperfect speech caused by bulbar disease have justly been distinguished from true aphasia by the use of other terms. Cases of complete aphasia in which all power of speech is lost, do little more than help us to ascertain the topographical position in the cortex of the 'speech' area, but cases of partial aphasia are especially instructive. Without attempting to go into the details of the subject and into the many considerations which have to be had in mind in dealing with it, for there are different kinds of aphasia, we may venture to say that the striking feature of partial aphasia is the failure to say certain words or syllables, and the tendency to substitute some wrong word or syllable for the right one. The words or syllables which are uttered are rightly pronounced without defect of articulation; and in many cases, though the right word cannot be produced as a direct effort of the will, it may be uttered under the influence of an emotion, or indeed sometimes as the result of some psychical processes more complex than those involved in the mere volitional effort to say the word. An instructive case is recorded of a man suffering from slight aphasia, who after several failures to say the word 'no' by itself, at last said, "I can't say no, sir."

From the phenomena of partial aphasia we may draw the deduction that the cortical speech area does not carry out the whole of the coordination of the impulses involved in articulation. That coordination is exceedingly complex, and we ought perhaps to recognize in it more than one degree or kind of coordination. The failure of articulation in disease of the bulb shews that a certain amount of coordination takes place there; for the affections of speech due to bulbar disease are not the same as those resulting from the mere loss of this or that muscle or nerve. We must of course admit that some, possibly a great deal, of coordination of a certain kind takes place in the cortex, for the bulb cannot by itself be made to speak; exactly how much, the knowledge at present at our disposal leaves a matter of great uncertainty; but it is sufficient for our present purpose to recognize that whatever may be the nature of the events taking place in the cortical area during the act of speech, those events make use of the machinery already provided in the bulb. The word spoken does not start, so to speak, ready made in the cortex; it is not that a group of impulses start from the cortex with their coordination fully achieved, and pass along certain nerve fibres to certain muscles, making their way without change through the tangle of the bulb, as if this were merely a bundle of lines offering paths for, but exercising no influence over the impulses. We must rather suppose that something takes place in the cortex of the third frontal convolution, as the result of which efferent impulses pass along the appropriate fibres of the pyramidal tract to the bulb, and there start a series of events leading to the issue of the coordinated impulses by which the word is spoken.

§ **661.** We have no reason whatever to think that the cortical area for speech differs in its fundamental characters from other divisions of the motor region, and are justified in carrying on to other areas the deduction we have just drawn in connection with the speech area. With that end in view we may now turn back to the experimental results obtained on the dog, and it will make our discussion simpler if we take as an illustration some large area such as the forelimb area.

We have seen that stimulation of this area produces what we may, to start with, speak of simply as movements of the fore-limb; and guided by the analogy of speech in man we may confidently conclude that when the dog voluntarily moves the fore-limb, the act is carried out by means of events taking place in the forelimb cortical area. The simplicity of the electrical phenomena resulting from cortical stimulation, which we described in § 657, might at first sight lead us to conclude that the whole matter was fairly simple; and indeed some writers appear to entertain the conception that in a voluntary movement such as that of the fore-limb, all that takes place is that the 'will' stimulates certain cells in the cortical area causing the discharge of motor impulses along the pyramidal fibres connected with those cells, and that these motor impulses travel straight down the pyramidal tract to the motor fibres of the appropriate nerves, undergoing possibly some change at the place in the cord where the pyramidal fibre makes junction with the fibre of the anterior root, but deriving their chief if not their whole coordination from the cortex itself, that is to say, being coordinated at their very starting point. That such a view is untenable, and that the simplicity of the electrical phenomena is misleading is shewn by the following two considerations among others. On the one hand, as was shewn in a previous section, the coordination of movements may be carried out apart from the cortex, namely, in the absence of the hemispheres; and we can hardly suppose that there should be two quite distinct systems of coordination to carry out the same movement, one employed when volition was the moving cause, and the other when something else led to the movement. On the other hand, the analogy of speech justifies us in concluding that the cortical processes do take advantage of a coordination effected by the action of other parts of the nervous system.

Bearing this in mind, we may recall attention to the remarkable effects which result from removal of the area. These are twofold. In the first place, there is more or less complete paralysis of the limb; all the movements of the limb are for a time ineffective. It is not that purely voluntary movements are alone, so to speak, cut out, the reflex and other movements are also impaired or temporarily abolished, and as we have already said in many cases at least the sensations of the limb are interfered with. These troubles are of course in part the effects of the mere operative interference belonging to what we spoke of in § 582, as being of the nature of shock. But, even giving full weight to this consideration, there remains the fact that the cortical area is associated with the various coordinating and other nervous mechanisms belonging to the limb by such close ties that these are thrown into disorder when it is injured. And side by side with this we may put the remarkable fact previously stated, that during an abnormal condition of the cortical area stimulation of the area, instead of producing the appropriate movements confined to the limb, may give rise to movements of other parts culminating in epileptiform convulsions.

In the second place, this paralysis is temporary only, the voluntary movements are after a while regained, and that in spite of the fore-limb moiety of the pyramidal tract permanently degenerating along its whole length, neither it nor the cortical area ever being regenerated. This shews that whatever be the chain of events in the intact animal, it is possible for the 'will' of the animal to get at the muscles and motor mechanisms of the fore-limb by some other path than that provided by the appropriate cortical area and corresponding path of the pyramidal tract; and the facts previously recorded (§ 658) shew that that other part is not the corresponding part of the pyramidal system belonging to the other half of the hemisphere and indeed is not any part at all of the whole pyramidal system. The 'will,' whatever be the processes by which it takes origin, and wherever be the place where they are carried on, is able in the absence of the pyramidal system to produce its effect on the motor fibres of the brachial nerves by working on other parts of the central nervous system.

Hence while admitting as we must do that in the intact animal the cortical area and pyramidal tract play their part in carrying out voluntary movements, their action is not of that simple character supposed by the view referred to above. On the contrary, we are driven to regard them rather as links, important links it is true, but still links, in a complex chain. As we have already urged, we may probably speak of the changes taking place in the pyramidal fibres as being on the whole of the nature of efferent impulses; but we should be going beyond the evidence if we concluded that they were identical with the ordinary efferent impulses of motor nerves. And above all it must not be left unnoticed that the cortical area has close if not direct connections of a sensory nature with the part in whose movements it is concerned. This is shewn by the following remarkable results which may make their appearance when stimulation of the cortex is carried while the animal (dog) is in a particular stage of the influence of morphia. If a subminimal stimulus be found, that is a current of such intensity that applied to a motor area it will produce no movement, but if increased ever so slightly will give a feeble contraction of the appropriate muscles, it may be observed that a slight stimulus, such as gently stroking the skin over the muscles in question, will render the previous subminimal stimulus effective and so call forth a movement. Thus if the area experimented on be that connected with the lifting of the forepaw, and the subminimal stimulus be applied to the area at intervals, after several applications followed by no movements, a gentle stroke or two over the skin of the paw will lead to the paw being lifted the next time the stimulus is applied to the area. A similar result, but less sure and striking, may follow upon the stimulation of parts of the body other than the part corresponding to the area stimulated. Then again it has been observed that in certain other stages of the influence of morphia, the cortex and the rest of the nervous system are in such a condition that the application of even a momentary stimulus to an area leads not to a simple movement but to a long-continued tonic contraction of the appropriate muscles. Under these circumstances, a gentle stimulus, such as stroking the skin, or blowing on the face, applied immediately after the application of the electric stimulus to the area, suddenly cuts short the contraction, and brings the muscles at once to rest and normal flaccidity.

These experiments shew that the development of the processes in the cortex leading to the issue of what we have agreed to call efferent impulses along the pyramidal fibres is markedly affected by sensory impulses and especially by sensory impulses started in the skin overlying and corresponding to the muscles put into movement. How those sensory impulses reach the cortex we do not exactly know; but we have no evidence to shew that afferent, centripetal impulses can travel backwards so to speak along the pyramidal fibres; and it is more reasonable to suppose that the sensory impulses in question reach the cortex by the ordinary paths of sensory impulses, which we shall presently discuss. We may therefore take the results of the experiments as shewing how close is the connection of the motor area with the sensory mechanisms of the spinal cord and lower parts of the brain, and as illustrating the complexity of the chain of events by which the motor area brings about voluntary movements.

§ 662. We have above used the general phrase 'movements of the limb,' since in the dog it is not easy to pick out certain movements as being particularly skilled movements. In the monkey such a distinction is easier. In this animal, as we have said, recovery of voluntary movement also takes place after removal of a cortical area, or at least has done so in many cases; and while the phenomena immediately following removal on the whole resemble those witnessed in the dog, a certain order of recovery may be observed; the more skilled movements are the last to return. When for instance the arm area is removed, the delicate movements of the hand, of the thumb and finger, are the last to be re-established; and a condition of things may be met with in which the animal after removal, say of the arm area in the left hemisphere, uses by preference the left hand at a time when, if prevented from using that hand, he is able to use the right; that is to say, the recovery in the right limb after the removal of the area on the left side is nearly but not quite complete; the 'will' can gain access to the right hand, but not so easily as to the left hand, and this latter is used, though under ordinary circumstances it would not be used.

When we turn to man, in whom the great development of the pyramidal system and differentiation of the cortical area is paralleled by the prominence of skilled and trained movements, the analogy of the phenomena of speech, if it be true as clinical histories seem to shew that destruction by disease of the speech area of both sides causes permanent aphasia, would lead us to conclude that at least highly skilled voluntary movements are carried out by the pyramidal system and by that alone. But in reference to this it must be remembered that such a permanent aphasia may be due, not to mere loss of the pyramidal channel, not to the will being merely unable to gain access to lower coordinating mechanisms, but to the absence of the differentiated cortical grey matter, by reason of which absence the will cannot initiate the first processes of the act of speech; it may be that were it able to do so, the processes so started might in the absence of the pyramidal tract, find some other way to the bulbar mechanism as in the case of the unskilled movements of the dog. This point however clinical histories have not definitely settled. Moreover in dealing with the phenomena of the nervous system of man as revealed by disease, we meet in reference to the cerebral cortex the same difficulty that we dwelt upon in dealing with the spinal cord (§ 591). Lesions of the pyramidal system, of the internal capsule for instance, lead to the loss not only of skilled but of all voluntary movements; according to the character and position of the lesion this or that part of the body is wholly withdrawn from the influence of the will. And it is possible to maintain the thesis that man has become so developed as to his nervous system and the motor cortex, so accustomed to make use exclusively of the pyramidal system that the will has lost the power, still possessed by lower animals, to gain access by some path other than the pyramidal one to the immediate nervous mechanisms of movement. The data for forming a satisfactory conclusion as to this point are so few and uncertain that it would be unprofitable to discuss the question here; but we may venture to point out that, great as is the development of the cerebral cortex and the pyramidal system in man, that development is accompanied by a hardly less striking expansion of other parts of the brain not directly connected with the pyramidal system which we have previously seen reason to associate with the coordination of movements, for example the cerebellum. And indeed it is clear that, admitting the pyramidal tract to be the ordinary channel by which volitional impulses pass to, or by which the will gains access to, the motor mechanisms immediately associated with the anterior roots of this or that spinal nerve, we must also admit that those volitional impulses passing along the pyramidal tract, or at least some of the processes constituting the will, are in connection with, and thus are influenced by the condition of, other parts of the brain. When for instance a gymnast executes a skilled voluntary movement in which all his four limbs and other parts as well perhaps of his body are involved, it is probably the case that changes of the nature of efferent impulses sweep down his pyramidal tract, and that these impulses, starting in a definite order from his cortex, that is to say having undergone a certain amount of initial coordination at their very origin, meet with further coordination in the spinal grey matter, which serves as a set of nuclei of origin for the motor nerves concerned in the movement, before they issue as ordinary motor impulses along the anterior roots. But this is not all. Should the gymnast's semicircular canals happen to be injured and his cerebellum thereby be troubled, or mischief fall on some other part of the brain which like this has no direct connection with either the pyramidal tract or the motor cortex, the movement fails through lack of coordination, though both the cortex, the pyramidal tract, and the spinal motor mechanisms remain as they were before. Obviously the carrying out of a voluntary movement is a very complex proceeding, and the motor cortex with the pyramidal tract is only one part of the whole mechanism; so far from the whole business being confined to these it is perhaps no exaggeration to say that in each movement of the kind most parts of the whole brain have a greater or less share.

The exact nature of the part played by the cortex and the pyramidal tract in voluntary movements our present knowledge is inadequate to define. When we pass in review a series of brains from the lower to the higher and see how the pyramidal system is so to speak grafted on to the rest of the brain, when we observe how the increasing differentiation of the motor cortex runs parallel to the increasing possession of skilled educated movements, we may perhaps suppose that 'a short cut' from the cortex to the origins of the several motor nerves, such as is afforded by the pyramidal fibres, from the advantages it offers to the more primitive path from segment to segment along the cerebrospinal axis has by natural selection been developed into being in man the chief and most important instrument for carrying out voluntary movements; but, we repeat, it remains even in its highest development a link in a chain, and a knowledge of how the whole chain works is at present hidden from us.

We must not here wander into psychological problems, but may repeat that in the above discussion we have used the word 'will' in a general sense only. A man may be brought into a condition, for instance in certain hypnotic phases, in which he can carry out all the various skilled movements which he has inherited or which he has learnt; and yet, according to some definitions of the word 'will', those movements could not be said to be initiated by his will. It can hardly be doubted that in such cases the motor cortex and pyramidal tract play their usual part. But we may pass from such cases as these through others, until we come to cases where a skilled movement which has been learnt and practised by the working of an intelligent will, may continue to be carried out under circumstances which seem to preclude the intervention of any conscious will at all; and the transition from one case to another is so gradual, that it is impossible to suppose that there has been any shifting of the machinery employed for carrying out the movement. So that a volitional origin is not an essential feature of these so-called voluntary movements, and the machinery of the motor cortex and pyramidal tract is available for other things than pure volitional impulses.

§ **663**. The preceding discussion will enable us to be very brief concerning a question which has from time to time been much discussed, and which has acquired perhaps factitious importance, viz. the question as to how volitional impulses leading to voluntary movements travel along the spinal cord. The conclusion at which we have arrived, namely, that in the normal carrying out of voluntary movements the chief part is played by efferent impulses passing along the pyramidal tract, carries with it the answer that volitional impulses travel in the spinal cord along the pyramidal tract.

In the dog, in which the whole pyramidal tract crosses at the decussation of the pyramids, we should expect to find that a break in the pyramidal tract of one side of the cord at any point along its length caused loss of voluntary movement on the same side below the level of the break. And experiments as far as they go support this view. No one it is true has attempted to divide or otherwise cause a break in the pyramidal tract alone, leaving the rest of the cord intact; and indeed, even if an injury were limited to the area marked out as the pyramidal tract, fibres other than pyramidal fibres would be injured at the same time, since the tract is never a 'pure' one. But it has been found that a section of a lateral half of the cord, a lateral hemisection, or a section limited to the lateral column of one side has for one of its principal effects loss of voluntary movement on the same side in the parts supplied by motor nerves leaving the cord below the level of the section. We say 'one of its principal effects' because, besides the concomitant interference with sensations concerning which we shall speak presently, the loss of voluntary movement is not absolutely confined to the same side; there is some loss of power on the crossed side, at least in a large number of cases. We must not lay stress on this crossed paralysis because it is probably one of the effects of the mere operation, not a pure 'deficiency' phenomenon, and indeed appears soon to pass away. But taking into consideration what was said above concerning the effects of removing cortical areas, it is important to note that in the experience of many experimenters the loss of voluntary power on the operated side diminishes after a while, and that the animal if kept alive and in good health long enough appears to regain almost full voluntary power over the affected parts. In such cases, as in other operations on the central nervous system, there is no regeneration of nervous tissue; the two surfaces of the section unite by connective not nervous tissue, and the tracts which as the result of the section degenerate downwards or upwards are permanently lost. Hence even if we admit that in the intact animal a voluntary movement is chiefly carried out by means of efferent impulses passing along the pyramidal tract right down to the motor mechanisms of the cord immediately connected with the motor nerves, we must also admit that the 'will' under changed circumstances can find other channels for gaining access to the same mechanisms.

It has been further observed that if in the dog a hemisection be made at one level, for instance in the lower thoracic region of the cord, and then, after waiting until the voluntary power over the hind limb of that side has returned, a second hemisection, this time on the other side, be made at a higher level, this second operation is followed by results similar to those of the first; there is loss of voluntary power on the side operated on, with some loss of power on the crossed side, and as in the first case this loss of power not only on the same but also on the crossed side may eventually disappear. This shews among other things that the recovery after the first operation was not due to the remaining pyramidal tract doing the work of both. Further, the hemisection may be repeated a third time, the third hemisection being on the same side as the first, with at least very considerable return of power over both limbs. That is to say, under such abnormal circumstances voluntary impulses may, so to speak, thread their way in a zigzag manner from side to side along the mutilated cord until they reach the appropriate spinal motor mechanisms. Such an abnormal state of things does not however really militate against the view that under normal circumstances volitional impulses normally travel along the pyramidal tract; but it does shew, what indeed has already been shewn by the phenomena of strychnia poisoning, § 586, that in the central nervous system the passage of nervous impulses (using those words in the general sense of changes propagated along nervous material) is not rigidly and unalterably fixed by the anatomical distribution of tracts of fibres; in all such discussions as those in which we are engaged we must bear in mind that physiological conditions as well as anatomical continuity are potent in determining the passage of these impulses.

§ **664**. When we reflect on the great prominence of the pyramidal tract in the spinal cord of man as compared with that of the dog, we may justly infer not only that the pyramidal tract is under normal circumstances more exclusively the channel of volitional impulses in man than in such lower animals, but also, bearing in mind the discussion in a previous chapter, § 591, concerning the activities of the spinal cord of man, that the potential alternatives presented by the spinal cord of the dog are greatly reduced in that of man. And such clinical histories of disease or accidental injury in man as we possess support this conclusion. Lesions confined to one half of the cord, or even lesions confined to the lateral column of one half, appear to lead to loss of voluntary power on the same side, and the same side only, in the parts below the level of the lesion; and the same symptoms have been observed to accompany disease limited apparently to the pyramidal tract of one side. Moreover, though cases of recovery of power have been recorded, we have not such satisfactory evidence as in animals of the volitional impulses ultimately making their way along an alternative route; but here the same doubts may be entertained as were expressed in discussing the reflex acts of the cord in man.

When we say that the loss of voluntary power is seen on the side of the lesion only, we should add that this statement appears to apply chiefly to the thoracic and lower parts of the cord. We have seen that in man, in the upper regions of the cord, the pyramidal tract is only partly crossed; a variable but not inconsiderable number of the pyramidal fibres do not cross at the decussation of pyramids, but running straight down as the direct pyramidal tract effect their crossing lower down in the cervical and upper thoracic regions. Hence we should infer that a hemisection of, or a lesion confined to one side of the cervical cord, would affect the voluntary movements of the crossed side as well as of the same side, though not to the same extent. But we have no exact information as to this point. And indeed the purpose of the direct tract is not clear; there is no adequate evidence for the view which has been held that these direct fibres are destined for the upper limbs and upper part of the body; since they are the last to cross we should à priori be inclined to suppose that they were distributed to lower rather than higher parts.

§ 665. We may now briefly summarise what we know concerning voluntary movements. And it will be convenient to trace the events in order backwards.

Certain muscles are thrown into a contraction which even in the briefest movements is probably of the nature of a tetanus. In almost every movement more than one muscle as defined by the anatomists is engaged, and in many movements a part of several muscles is employed, and not the whole of each. It is perhaps partly owing to the latter fact that a muscle which has become tired in one kind of movement, may shew little or no fatigue when employed for another movement, though we must bear in mind that in a voluntary movement fatigue is much more of nervous than of muscular origin.

Besides the active muscles, if we may so call them, which directly carry out the movement, the metabolism of which supplies the energy given out as work done, other muscles, some of which are antagonistic to the active muscles and some of which may be spoken of as adjuvant, enter into the whole act. In flexion for instance of the forearm on the arm it is not the flexor muscles only but the extensors also which are engaged. According to the immediately preceding position and use of the arm, and according to the kind and amount of flexion which is to be carried out, the extensors will be either relaxed, that is to say inhibited, or thrown into a certain amount of contraction. And in some of the more complicated voluntary movements the part played by adjuvant muscles is considerable. Hence in a voluntary movement the will has to gain access not only to the active muscles, but also to the antagonistic and adjuvant muscles; and every voluntary movement, even one of the simplest kind, is a more or less complex act.

The impulses which lead to the contraction of the active muscles reach the muscles along the fibres of the anterior roots, (we may for the sake of simplicity take spinal nerves alone, neglecting the peculiar cranial nerves), and such evidence as we possess goes to shew that the impulses governing the antagonistic and adjuvant muscles travel by the anterior roots also; the question whether the inhibition of the antagonistic muscles when it takes place, is carried out by inhibitory impulses passing as such along the fibres, or simply by central inhibition of previously existing motor impulses need not be considered now. These anterior roots are connected as we have seen with the grey matter of the cord, and in each hypothetical segment of the cord we may recognize the existence of an area of grey matter which, though we cannot define its limits, we may, led by the analogy of the cranial nerves, call the nucleus of the nerve belonging to the segment; and we may further recognize in such a nucleus what we may call its efferent and its afferent side.

Every voluntary movement, even the simplest, is as we have repeatedly insisted a coordinated movement, and in its coordination afferent impulses play an important part. The study of reflex actions, § 589, has led us to suppose that each spinal segment presents a nervous mechanism in which a certain amount of coordination is already present, in which efferent impulses are adjusted to afferent impulses. But the results obtained by stimulating separate anterior nerve roots shew that, in the case of most muscles at all events, the especially active muscles of the limbs for instance, each muscle is supplied by fibres coming from more than one nerve root, that is to say the spinal nucleus, or at least the spinal motor mechanism for any one muscle, extends over two or three segments. Hence à fortiori in a voluntary movement, involving as this does in most cases more than one muscle, the spinal mechanism engaged in the act spreads over at least two or three segments, thus allowing of increased coordination. In that coordination the impulses serving as the foundation of muscular sense play an important part, but other afferent impulses, such as those from the adjoining skin, also have their share in the matter; and it is worthy of notice that not only is the skin overlying a muscle served, broadly speaking, by nerve roots of the same segment as the muscle itself, afferent in one case, efferent in the other, but in the parts of the body where coordination is especially complex, in the fingers for instance, not only is each muscle supplied from more than one segment, but also each piece of skin is supplied in the same way by the posterior roots of more than one nerve.

In the case of the frog it is clear that in reflex movements a large amount of coordination is carried out by these various spinal mechanisms; and as we have urged, we may safely infer that in the voluntary movements of the frog, the will makes use of this already existing coordination, whatever be the exact path by which in this animal the will gains access to the spinal mechanisms. In the dog we may conclude that in voluntary movements the spinal mechanisms, with coordinating functions, are also set in action, in this case by impulses passing straight from the cortex to the mechanisms by the pyramidal tract, though apparently, in the absence of the pyramidal tract, the will can work upon the mechanisms by changes travelling through other parts of the cerebrospinal axis. And in the monkey and man, subject to the doubts already expressed as to the potentialities of the human spinal cord, we may probably also infer that in each voluntary movement some, perhaps we may say much, of the coordination is carried out by the spinal mechanism set into action through impulses along the pyramidal tract. We may probably further infer that a careful adjustment obtains between the beginnings of the pyramidal tract in the cortex and its endings in the cord, so that the topography of 'areas' or 'foci' in the cortex above is an image or projection of the spinal mechanisms below.

The complex character, on which we insisted just now, of almost every voluntary movement necessitates that in every such movement a large area of spinal mechanism is involved. But this is not all. The movements of any part, of the legs for instance, are not determined, nor is the coordination of the movements effected, simply by what is going on in the legs and the part of the spinal cord belonging to them. The discussion in a previous section has shewn that much of the coordination of the body is carried out by the middle portions of the brain, and on these the motor area must have its hold as well as on the spinal mechanisms.

The details of the nature of that hold are at present unknown to us; but it must be remembered that not all the fibres passing down from the motor region, not all those even proceeding from the densest and most clearly defined motor areas, are pyramidal fibres. With the pyramidal fibres are mingled fibres having other destinations, and some of these probably pass to the thalamus and so join the great tegmental region. Moreover the motor region must have close ties with other regions of the cortex whence as we have seen, § 632, fibres pass to the pons to make connections with the cerebellum. On the other hand, as we have seen, § 612, the cerebellum is especially connected with what we may fairly consider the afferent side of the spinal cord and bulb. These facts must merely be taken as indicating the possibilities by which the motor region is kept in touch with the great coordinating mechanism; it would be venturesome at present to say much more.

In an ordinary voluntary movement an intelligent consciousness is an essential element. But many skilled movements initiated and repeated by help of an intelligent conscious volition may, when the nervous machinery for carrying them out has acquired a certain facility, (and in all the higher processes of the brain we must recognize that, in nervous material at all events, action determines structure, meaning by structure molecular arrangement and disposition) be carried out under appropriate circumstances with so little intervention of distinct consciousness that the movements are then often spoken of as involuntary. All the arguments which go to shew that the distinctly conscious voluntary skilled movement is carried out by help of the appropriate motor area, go to shew that the motor area must play its part in these involuntary skilled movements also. So that distinct consciousness is not a necessary adjunct to the activity of a motor area. And it is worthy of notice that some of these, in their origin, purely voluntary skilled movements, which by long-continued training have become almost as purely involuntary, are hampered rather than assisted by being "thought about."

The word 'training' suggests the reflection that the physiological interpretation of becoming easy by practice is that new paths are made, or the material of old paths made more mobile by effort and use. We have already urged, § 581, that the grey matter of the spinal cord is a network, in which the passage of impulses is determined by physiological conditions rather than anatomical continuity, and the same considerations may with still greater force be applied to the brain. We must suppose that training promotes the growth and molecular mobility of the motor area and of all its connections. There are doubtless limits to the changes which can be effected, but within these limits the will, blundering at first in the maze of the nervous network, gradually establishes easy paths; though even to the end it blunders, in trying to carry out one movement it often accomplishes another.

Lastly, without attempting to enter into psychological questions, we may at least say that the birth-place of what we call the 'will,' is not conterminous with the motor area; the will arises from a complex series of events, some of which take place in other regions of the cortex, and probably in other parts of the brain as well. With these parts the motor area has ties concerned not in the carrying out of volition, but in the generation of the will. So that, looking round on all sides, it is obvious, as we have said, that the motor area is a mere link in a complex chain. It is moreover a link of such a kind, that while the changes which the breaking of it makes in the daily life of a lowly animal, such as the dog, in whom the experience of the individual adds relatively little to the nervous and psychical storehouse transmitted from his ancestors, can hardly be appreciated by a bystander, those which the breaking of it makes in the daily life of a man, whose brain at any moment is not only a machine fitted for present and future work but a closely packed record of his past life, are obvious not only to the individual himself, but to his fellows.

SEC. 8. ON THE DEVELOPMENT WITHIN THE CENTRAL NERVOUS SYSTEM OF VISUAL AND OF SOME OTHER SENSATIONS.

Visual Sensations.

§ 666. In the chain of events through which some influence brought to bear on the periphery of a sensory nerve gives rise to a sensation, we are able, with more or less success, to distinguish between those events which are determined by the changes at the periphery and those which are the expression of changes induced in the central nervous system. Thus when certain rays of light proceeding from an object and falling upon the eye give rise to visual perception of the object, two sets of events happen; the rays of light, by help of the mechanisms of the eye, partly dioptric, partly nervous, give rise to certain changes in the fibres of the optic nerve, which we may call visual impulses; and these visual impulses reaching the brain along the optic nerve give rise to visual sensations and so to visual perception of the object. We shall later on, under the heading of "the senses," deal chiefly with the peripheral events, and have now to consider some points connected with the central events, to learn what we know concerning how the various sensory impulses travelling along the several kinds of sensory nerves behave within the central nervous system. In doing so we shall have from time to time to refer to peripheral events, but only occasionally, and never in any great detail. It will be convenient to begin with the special sense of sight, and we must first briefly call attention to a few points which we shall have to study in fuller detail hereafter.

The eye is so constructed that images of external objects are brought to a focus on the retina, the stimulation of which by light starts the visual impulses along the fibres of the optic nerve; and the distinctness with which, by means of the visual sensations arising out of these visual impulses, we perceive external objects is dependent on the sharpness of the retinal images. The eye is further so constructed that, in any position of the eye, the rays of light proceeding from a portion only of the external world fall upon the retina; or in other words in any one position of the eye only a portion of the external world is visible at the same time. The portion so seen is spoken of as the *visual field* for that position.

The image thrown on the retina is an inverted one, so that the top of an actual object is represented by the lower, and the bottom by the upper part of the retinal image; similarly the actual left hand side of the retinal image corresponds to the right hand side of the actual object, and the right hand side to the left hand side. Hence the right hand half of the visual field corresponds to the left hand side of the retina, and the left hand half to the right hand side.

The eye can be moved in various directions, and since in the visual field the portion of external nature which can be seen at the same time differs with each different position, a large range of vision is thus secured; and this can be further increased by movements of the head. Moreover we normally make use of two eyes, our normal vision is binocular; and the visual field of the right eye differs from that of the left eye. There is one striking difference which must always be borne in mind. A section carried through the eye in a vertical and front-to-back plane, through what we shall learn to call the optic axis (Fig. 133, *ox*) (the exact details of the plane may be left for the present), will divide the retina into two lateral halves, and in each retina one half will be on the nasal side next to the nose, and the other half will be on the malar or temporal side, next to the cheek or temple. It must be remembered that the nasal halves and temporal halves of the two retinas do not occupy corresponding positions in space. The temporal half of the left retina is on the left side of its own eye, whereas the temporal half on the right retina is not on the left but on the right side of its eye; and so with the nasal halves. Now, in the right eye, the right hand side of the visual field corresponds to the nasal half of the retina, and the left hand side of the visual field to the temporal half of the retina, whereas in the left eye the right hand side of the visual field corresponds to the temporal half of the retina, and the left hand side to the nasal half. This is shewn in Fig. 133, where the left hand visual field and the retinal area concerned are shewn shaded in each eye.

When we look at an object with the two eyes, though two retinal images are produced, one in one eye and one in the other, we perceive one object only, not two. This is the essential fact of binocular vision; when certain parts of each retina are stimulated at the same time we are conscious of one sensation only, not two; and the parts of the two retinas which, stimulated at the same time, give rise to one sensation are spoken of as "corresponding parts." From the structure and relations of the two eyes it follows that the temporal side of the right and the nasal side of the left eye are such corresponding parts, while the nasal side of the right eye corresponds to the temporal side of the left eye. But the whole

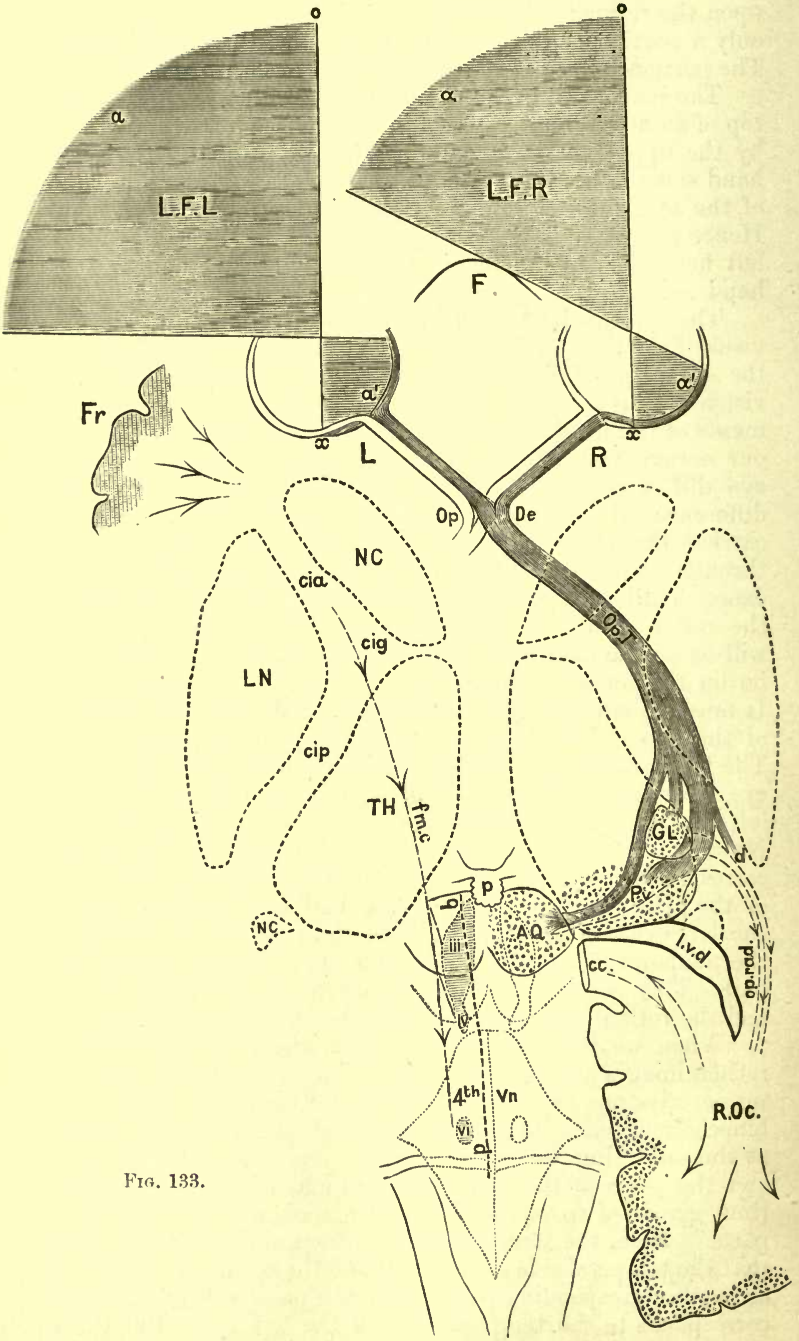
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Fig. 133.

FIG. 133. DIAGRAM TO ILLUSTRATE THE NERVOUS APPARATUS OF VISION IN MAN. (Sherrington.)

L. the left eye, *R.* the right eye, *o.x.* the optic axis. *F.* the outline of the face between the eyes, *Op.T.* the right optic tract (shaded) supplying, through *Op. De.* the optic decussation, the temporal side of the retina of the right eye and the nasal side of the retina of the left eye. *L. F. L.* and *L. F. R.* the left visual fields of the left and right eye respectively; the two fields and the parts of the two retinas whose excitation produces vision over the fields are shaded, the object *a* in the field of the right side giving rise to an image at *a′*, and *a* on the left side an image at *a′*.

The right optic tract is represented as ending in *GL.* the lateral corpus geniculatum, in *Pv.* the pulvinar, and in *AQ.* the anterior corpus quadrigeminum, all three stippled; *op. rad.* the optic radiation from these bodies to *R. Oc.* the right occipital lobe, whose stippled cortex indicates the "visual area." *d.* the 'direct' tract to the cortex. *c. c.* corpus callosum, cut across at the splenium, *l. v. d.* descending horn of the lateral ventricle.

The left side has been utilized to indicate at *F.* shaded with lines, the cortical motor area for the eyes; *fm. c.* indicates the path from it to III. IV. VI. the nuclei of the third, fourth and sixth nerves. *p. b.* the posterior longitudinal bundle, shewn as a broken line. *NC.* the nucleus caudatus, *LN.* the nucleus lenticularis and *TH.* optic thalamus shewn in outline, *Cia.* the front limb, *Cig.* the knee, and *Cip.* the hind limb of the internal capsule. The outlines of the fourth ventricle 4th *Vn.* and of the posterior corpora quadrigemina are shewn by dotted lines, that of the bulb is shewn by a fine line. *p.* the pineal gland.

of each retina is not employed in binocular vision. Owing to the position of the two eyes in relation to the nose, it comes about that an object held very much on one side, to the left hand side for instance, while it is capable of producing an image on the extreme nasal side of the left eye, and can be seen therefore by that eye, cannot produce an image on the temporal side of the right eye; the nose blocks the way. It is therefore not seen by the right eye, and the vision of it is monocular, by the left eye only. In Fig. 133 it may be seen that the left visual field of the left eye (*L.F.L*) extends more to the left, and is larger than the left visual field of the right eye, *L.F.R* and that the right retinal area, corresponding to the left visual field, extends farther along the nasal side of the left side (*a′*), than it does along the temporal side of the right eye (*a′*), the difference being due to the presence of the nose (*F*). And similar conditions obtain with regard to the extreme right hand side of the visual field.

§ 667. After these preliminary statements, we may now turn to consider some anatomical facts concerning the ending of the optic nerve in the brain.

The optic nerve of each eye consists of nerve fibres coming from all parts of the retina of that eye; but the two optic nerves meet, ventral to the floor of the third ventricle, cross each other at the *optic chiasma* (Fig. 133, *op. De*), and are thence continued on under the name not of optic nerves but of *optic tracts* (*Op.T.*). The decussation of fibres which takes place in the chiasma has peculiar characters. At their decussation (we are speaking now of man) the fibres in the optic nerve belonging to the temporal half of the eye in which the nerve ends pass into one optic tract, namely, the optic tract of the same side, while the fibres belonging to the nasal half pass into another optic tract, namely, the optic tract of the opposite side. Thus the fibres of the temporal half of the right eye and of the nasal half of the left eye pass into the right optic tract, and the fibres of the nasal half of the right eye and of the temporal half of the left eye pass into the left optic tract. Compare Fig. 133, in which the fibres forming the right optic tract are shaded while those forming the left optic tract are left unshaded. Now, the nasal half of one retina and the temporal half of the other retina are 'corresponding' parts. Hence, while each optic tract contains fibres belonging to half of each eye, the two halves thus represented in each tract are corresponding halves.

The amount and character of the decussation taking place in the optic chiasma differs in different animal types, the differences having relation to the amount of binocular vision, which in turn depends on the position of the eyes in the head, that is, on the prominence of the face between the eyes. In the fish for instance, with laterally placed eyes, no binocular vision at all is possible, and the decussation is complete; the whole optic nerve of each eye crosses over to the other optic tract. Between this and the arrangement in man just described, various stages obtain in various animals.

The chiasma also contains at its hinder part fibres which have no connection with the optic nerves or the eyes, but are simply commissural tracts passing from one side of the brain, namely from the median corpus geniculatum (§ 630) along one optic tract, through the chiasma to the other optic tract, and so to the median corpus geniculatum of the other side of the brain. These fibres are spoken of as the *inferior* or posterior (optic) *commissure* or arcuate commissure, or Gudden's commissure. It was once thought that in a similar way fibres passed from one retina along one optic nerve, through the front part of the chiasma to the other optic nerve, and so to the other retina forming an anterior (optic) commissure; but this seems to be an error.

§ **668**. The optic vesicle is as we have seen budded off from the fore-brain or forerunner of the third ventricle, and the optic chiasma is attached to and forms part of the floor or ventral wall of that ventricle. In a view of the basal or ventral surface of the brain the diverging optic tracts are seen to separate the anterior perforated space and lamina cinerea in front from the posterior perforated space, tuber cinereum with the infundibulum, and corpora albicantia behind, all these being parts of the floor of the third ventricle. From the grey matter in this floor fibres, forming what is sometimes spoken of as Meynert's commissure, belonging neither to the optic nerves nor to the inferior commissure, join the optic tracts, eventually leaving them to pass to the pes. Hence the whole of the optic tract is by no means derived from the optic nerve, the fibres just mentioned and the inferior commissure form parts of the optic tract not connected with the retina.

Each optic tract crosses obliquely, being in crossing firmly attached to, the ventral surface of the crus cerebri of the same side, Fig. 108 *C*, and is soon lost to view, being covered up by the temporo-sphenoidal lobe of the hemisphere. When this is removed the tract is seen to sweep dorsally round the crus, towards the dorsal aspect, and as we have already (§ 630) said to become connected on the farther side of the crus with the two *corpora geniculata*, lateral and median. We may say at once that the median corpus geniculatum has no connection with that part of the tract which is derived from the optic nerve, and is not concerned in vision, but is connected with that part of the tract, sometimes called the median part, which goes to form the inferior commissure. We may confine our attention to that part of the tract which consists exclusively of fibres coming from the retinas of the two eyes, for it is this part, and this part only, which is concerned in vision.

§ 669. This ends in three main ways, as shewn diagrammatically in Fig. 133. In the first place part of the tract ends in the lateral corpus geniculatum (*GL*), formed of alternating layers of white and grey matter, the grey matter containing in some parts large nerve cells, and in others small nerve cells. In these cells, of one kind or another, many of the fibres appear to end. In the second place, a very large number of fibres passing the corpus geniculatum on its ventral and lateral surfaces spread out into the pulvinar (*PV*). In the third place others, in considerable number, taking a more median direction, reach the anterior corpus quadrigeminum (*AQ*). These two sets also, like the first, end apparently in the nerve cells of the respective bodies. Thus the really optic fibres of the optic tract end in one of three collections of grey matter, the lateral corpus geniculatum, the pulvinar, and the anterior corpus quadrigeminum. Further, we have reasons for thinking that a considerable part at all events of the grey matter of these three bodies is associated with and, in a certain sense, dependent on the fibres of the optic nerves; the reasons are as follows. We know that when a nerve fibre is cut away from its trophic centre it degenerates; but the division, and the loss of the peripheral degenerating portion, has no obvious effect on the trophic centre; when a spinal nerve, for instance, is divided below the spinal ganglion, though the nerve below the section degenerates, the ganglion and the piece of nerve in connection with it remain very much as before. We have it, however, in our power to bring about changes of a deeper and wider character, a cessation of growth amounting to atrophy, by operative interference with nervous structures before they are fully developed. Thus in an adult animal, a section of an optic nerve or removal of the eye leads to degeneration in the optic nerve and optic tract; the optic fibres have their trophic centre in certain cells of the retina, of which we shall speak in treating of vision, and cut away from that centre they degenerate; by this means the nature of the optic decussation in animals, and indeed in man, has been ascertained. But if the eyes be removed (removal of both eyes being desirable on account of the characters of the optic decussation), in a new-born animal, not only do both the optic nerves and the greater part of both optic tracts cease to be further developed and degenerate, but the bodies mentioned above, the two lateral corpora geniculata, the pulvinar on each side, and the two anterior corpora quadrigemina do not fully develope; certain parts of them undergo atrophy. The development of these nervous structures seems therefore to be largely dependent on their functional connection with the eyes by means of the optic tracts and nerves.

The same method confirms the view expressed above that the median corpus geniculatum has no connection with vision. When the eyes of new-born animals are extirpated neither the median corpora geniculata nor the posterior corpora quadrigemina shew any sign of atrophy, and the part of the optic tract which does not degenerate is the inferior commissure connecting the two median corpora geniculata. Obviously these parts are associated with functions of the brain other than those of sight. The lateral corpora geniculata, the pulvinar and the anterior corpora quadrigemina, are, we may repeat, alone to be regarded as the chief central parts in which the optic nerves end. We may also repeat that owing to the peculiarity of the optic decussation each optic nerve thus finds its endings in both sides of the brain.

While the optic chiasma is, as we have seen, helping to form the floor of the third ventricle, it gives off fibres to the posterior perforated spot. Some of these have been supposed to pass directly in the wall of the ventricle to the nucleus of the third (oculo-motor) nerve, and to serve as a channel for afferent impulses, causing constriction of the pupil; but to this we shall return in dealing hereafter with the movements of the pupils.

§ 670. Though the above three bodies are undoubtedly the chief endings of the optic nerve, three primary visual centres, if we may so call them, it is also believed that some fibres of the optic tract, making connections with neither of these three bodies, pass by the crus cerebri straight to certain parts of the cerebral hemisphere (Fig. 133, *d*); but this fourth ending is by no means so clearly established as are the other three.

And undoubtedly the main connection of the cerebral hemisphere with the optic tract is not a direct one, but an indirect one, through the three bodies in question. We said, § 633, that fibres proceeding from the occipital cortex and reaching the thalamus through the hind limb of the internal capsule formed what was called the 'optic radiation.' These fibres beginning (or ending) in the cortex of the occipital region, end (or begin), (Fig. 133, *op. rad*) to a large extent in the pulvinar and in the lateral corpus geniculatum, but also in the anterior corpus quadrigeminum, reaching it by the anterior brachium (§ 634). When even in a grown animal the occipital cortex is destroyed, not only these fibres but also parts of the pulvinar and external corpus geniculatum undergo degeneration, and there is some change in the anterior corpus quadrigeminum. When the same cortex is destroyed in a new-born animal the same parts atrophy; and in such cases the optic tract and nerve, which are but little affected by the operation in the adult animal, are also involved in the atrophy. We may add that removal of both eyes in the new-born animal is said to lead, besides the atrophy of the three bodies in question, to a diminished occipital lobe due to lack of white matter. We may therefore conclude that in the complex act of vision two orders of central apparatus are involved; we may speak of two kinds of centres for vision, the primary or lower visual centres supplied by the three bodies of which we are speaking, and a secondary or higher visual centre supplied by the cortex in the occipital region of the cerebrum. And experimental results accord with this view.

Before we proceed to discuss those results, one or two preliminary observations may prove of use.

In the first place, as we have previously urged, the interpretation of the results of an experiment in which we have to judge of sensory effects, are far more uncertain than when we have to judge of motor effects, that is of course when the experiment is conducted on an animal. We can estimate the motor effect quantitatively, we can measure and record the contraction of the muscle; but in estimating a sensory effect we have to depend on signs, our interpretation of which is based on analogies which may or may not be misleading. We are on safer ground when we can appeal to man himself in the experiments instituted by disease; but the many advantages thus secured are often more than counterbalanced by the diffuse characters, or the complex concomitants of the lesion. In dealing with sensory effects we must expect and be content for the present with conclusions less definite and more uncertain even than those gained by the study of motor effects.

In the second place, in dealing with vision, it will be desirable to know the meaning which we are attaching to the words which we employ. By blindness, that is 'complete' or 'total' blindness, we mean that the movements and other actions of the body are in no way at all influenced by the amount of light falling on the retina. Of partial or incomplete or imperfect vision, using the word vision in its widest sense, there are many varieties; and we may illustrate some of the defects of the visual machinery, regarded as a whole, with its central as well as its peripheral parts, by referring to certain defects of vision due to changes in the eye itself. The eye may fall into such a condition, that the mind can only appreciate, and that to a varying degree, the difference between light and darkness; the mind is aware that the retina (or it may be part of the retina) is being stimulated to a less or greater degree, but cannot perceive that one part of the retina is being stimulated in a different way from another part; a sensation of light is excited, but not a set of visual sensations corresponding to the sets of pencils of luminous rays, which, reflected, or emanating from external objects in a definite order, are falling upon the eye. The eye again may fall into another condition, in which such sets of visual sensations are excited, but on account of dioptric imperfections or for other reasons, the several sensations are not adequately distinct; the mind is aware through the eye of the existence of 'things,' but cannot adequately recognize the characters of those things; the visual images are blurred and indistinct. And a large number of gradations are possible between the extreme condition in which only those objects which present the strongest contrast with their surroundings are visible, to a condition which only just falls short of normal vision. Imperfections of this kind, of varying degree, may result from failure not in the peripheral apparatus, not in the retina, or optic nerve or other parts of the eye, but in the central apparatus; the retinal image may be sharp, the retina and the optic fibres may be duly responsive, but from something wrong in some part or other of the brain, the visual sensations excited by the visual impulses may fail in distinctness, and that in varying degree: imperfections of vision whether of central or peripheral origin, in which visual sensations fail in distinctness are generally spoken of under the not wholly unexceptionable name of *amblyopia*.

If one optic nerve be divided, total blindness of one eye will result; but if one optic tract be divided, it follows from what has been said above, that half-blindness in the corresponding halves of both eyes will result. If, for instance, the right optic tract (Fig. 131, *Op. T.*) be divided, the *left* visual fields of both eyes will be blotted out. The same condition will be brought about by failure in the optic tract at its central ending, provided of course the mischief be confined to the ending of the one tract. Such a half-blindness or half-vision is spoken of as *hemianopsia*, or *hemianopia* or *hemiopia;* the words left and right are generally used in reference to the visual field; thus left hemianopsia is the blotting out of both left visual fields, through failure of the right optic tract.

If instead of the whole optic nerve being divided, certain bundles only were cut across, partial blindness would be the result, a portion of the visual field would be blotted out; and mischief limited to a few bundles of one optic tract would lead to corresponding blots in the corresponding halves of the visual fields of both eyes.

Further, an affection of half the retina or of a limited area in the retina might occur of such a character as to lead not to complete, but to partial blindness, to a hemi-amblyopia or to a partial amblyopia. The part of the retina so affected might be central, or peripheral, or a quadrant, or any patch of any size, form and relative position. And we may further imagine it at least possible that mischief in the brain might be so limited as to produce any of the above partial effects, though the retina, optic nerve, and optic tracts all remained intact.

The above visual imperfections we have illustrated by changes in the peripheral apparatus, but there is a kind of imperfection which we may still call a visual imperfection, though it is of purely central origin. In a normal state of things a visual sensation, excited in the brain, is or may be linked on to a chain of psychical events; we often then speak of it as a visual idea. When we see a dog, the visual sensation, or rather the group of sensations making up the visual perception of the dog, does not exist by itself, apart from all the other events of the brain; it joins and affects them, and among the events which it so affects may be and often are psychical events; the visual perception 'enters into our thoughts' and modifies them. Between the visual impulse as it travels along the optic nerve or tract and its ultimate psychical effect a whole series of events intervene; and we may take it for granted that the chain may be broken or spoilt at any of its links, at the later as well as at the earlier ones. We may therefore consider it possible that the break or damage may occur at the links by which the fully developed visual sensation joins on to psychical operations. We may suppose that an object is seen and yet does not affect the mind at all or affects it in an abnormal way.

These foregoing considerations emphasize the difficulty and uncertainty of interpreting the visual condition of an animal which has been experimented upon. When for instance, after an operation, an animal ceases to be influenced in its previous normal manner by the visual effects of external objects, a most careful psychical analysis is often necessary to enable us to judge whether the newly introduced disregard of this or that object is due to the mere visual sensations being blurred or blunted, or to some failure in the psychical appreciation of the sensations; and in most cases such an analysis is beyond our reach. The greatest caution is needful in drawing conclusions from experiments of this kind, especially from such as appear to have been hastily carried out or hastily observed; and we must be content here to dwell on some of the broader features only of the subject.

§ **671.** Since we have in this matter to trust so much to analogies with our own experience, we may turn at once to the monkey, as being more instructive than any of the lower animals. We have already said that electrical excitation of the occipital cortex behind the motor region may produce movements, but that these movements are in character different from those caused by stimulation of the motor region itself. In the monkey stimulation of parts of the occipital region, the occipital lobe and the angular gyrus for instance, may give rise to movements of the eyes, of the eyelids, and of the head, that is of the neck, all the movements so produced being such as are ordinarily connected with vision. It will not be profitable to enter here into the details concerning the exact topography of the excitable parts or of the special characters of the movements so called forth. But it is important to note that these movements are unlike the movements excited by stimulation of the appropriate motor area in as much as their occurrence is far less certain, they need a stronger stimulus to bring them out, when evoked they are feeble, being easily antagonized by appropriate stimulation of the motor area, and they have a much longer latent period. They are not due to any indirect stimulation of the motor area, through "association" fibres connecting the spot stimulated with the motor area or otherwise, since they persist after removal of the motor area. Movements of this kind may also be witnessed in the dog. They are obviously the result of impulses transmitted in some direct manner from the cortex to some parts below, and may be taken as an indication that the parts of the cortex in question are in some way connected with vision. The exact manner however in which they are brought about is at present obscure. The explanation of their genesis which is frequently offered, namely that the stimulation so affects the cortical grey matter as to give rise to visual sensations, and that the movements express these sensations, does not seem satisfactory. For, if it be possible that the gross changes which the electric current sets going in the cortical grey matter can reproduce the psychical events which take place in that grey matter in the normal action of the brain, we should expect stimulation of any and every part of the cortex to call forth some movement or other, since it cannot be doubted that every part of the cortex is in some way or other engaged in psychical operations, and that every psychical phase tends to express itself in movement. Whereas outside the motor region, with the exceptions we are now discussing, the cortex is, as we have seen "inexcitable," and even within the motor region itself the excitable substance is scattered, with increasing segregation as we advance along the animal scale, among inexcitable substance. When we speak of the region, or substance as inexcitable, we do not mean that the electric current produces no effect; we only mean that the effect is not manifested by movement; the real difference between the excitable motor region and the inexcitable rest of the cortex is probably that in the several motor areas the current, playing upon the beginnings of the pyramidal fibres, is able to inaugurate simple motor impulses or something like them, whereas elsewhere the molecular changes induced by the current are too confused to reach their normal expression. There can be no doubt of course that molecular changes in this or that part of the brain, set going by processes other than actual visual impulses along the optic nerves, may give rise to visual sensations; and as we shall see in dealing with the senses the subject of such 'subjective' sensations is unable to distinguish them from sensations of 'objective' origin; but it is at least unlikely that the coarse disturbances started by a tetanizing current should take such a definite form. Moreover the view in question is disproved by the experimental result that the same movements are brought about when the cortex is pared away and the electrodes are applied to the subjacent white matter. This result suggests the existence of efferent tracts or bundles of a special kind, differing from those of the pyramidal kind, though like them making connections with the ocular and other muscles; we have, however, as yet no other evidence of such tracts existing.

§ **672**. The results of removal of the cortex also support the same general conclusion, though there is much discordance among the various observers both as to the particular results and especially as to their interpretation. One broad fact comes out in all the observations, namely, that removal of or injury to the hind region of the cortex always produces some disturbance of vision, and produces disturbance of vision more surely and to a greater extent than does injury to or removal of any other region of the cortex; but beyond this broad fact there is much dispute, and we must be content here with a very brief statement.

In the monkey some observers have found that removal of the occipital lobe on one side, the region marked "vision" in Figs. 126, 127, caused hemiopia, the effect on the visual fields being a crossed one; when the right lobe was removed there was blindness in the left visual fields, that is in the right halves of the retinas of both eyes; in other words the visual impulses passing along the right optic tract failed to produce their usual effect, so that the animal disregarded objects on its left hand side. We may remark that the decussation of the optic nerves in the monkey is very similar to that in man. When both occipital lobes were removed, total blindness resulted. But, and this is most important, not only was the hemiopia, caused by the removal of one lobe, transient, but also, according to some observers, the lost vision returned after the total removal of both lobes, though some impairment might be noticed long afterwards, so long in fact as the animal was kept alive.

In the hands of other observers destruction of the angular gyrus of one side (Fig. 125) has led to hemiopia, failure in the left (or right) visual fields, indicating failure in the central endings of the right (or left) optic tract, being caused by removal of the right (or left) gyrus, and destruction of both angular gyri has led to total blindness, not only the hemiopia but the total blindness being, however, apparently transitory. And cases have been observed in which the transient blindness due to removal of the occipital lobes has been succeeded by permanent hemiopia upon the subsequent removal of the angular gyrus. Indeed the general, but not uniform, tendency of the many experiments which have been made is to connect, in the monkey, both the occipital lobe, and the angular gyrus with vision.

In the dog, removal of portions of the occipital cortex have also led to partial and transient blindness, or according to some to permanent blindness; but the difficulties of judging of the visual condition of a dog are very considerable, and his vision is so different from that of man, so much less binocular, for instance, than his, that it would not be profitable to relate at length the results obtained in the dog, or to discuss the conclusions which have been derived from them. We will only say that some observers have been led to think that the lateral part of the retina is connected with the lateral part of the visual occipital area, the front part with the front part and so on, the retina being as it were projected on to the occipital cortex; but the facts are not clear enough to make it worth while to dwell upon them here.

In man clinical histories so far conform to the results of experiments on the monkey as to associate the occipital cortex, and more particularly the cuneus (see Figs. 129, 130) with vision. They have however raised a point on which we have not yet touched. In the experiments on the monkey, quoted above, the result (putting aside transient effects due probably to "shock") of interference with one side of the brain was hemiopia; and this is what we might expect from the anatomical relations; the optic tract goes straight to the tegmental masses of its own side, and the optic radiation passes from those masses to the occipital cortex of the same side; there is no decussation save of the fibres of the optic nerve, as they pass into the optic tract at the chiasma. Clinical histories teach the same lessons as these experiments on animals; lesions limited to the occipital lobe, have for a symptom, hemiopia; and this is said to be especially the result of mischief limited to the apex of the occipital lobe, that is, to the cuneus. But experiments on monkeys have been made in which destruction of one angular gyrus has produced, not hemiopia, but crossed blindness or crossed amblyopia, that is to say has affected the whole of the retina of one eye, and that the crossed eye, the eye of the same side not being, or being supposed not to be, at all affected; similar results have also been stated to follow upon removal of one occipital lobe. And a few clinical cases have been recorded in which disease, especially of the angular gyrus, seemed to affect the vision of the whole of the crossed eye. (It must be remembered that the angular gyrus of man corresponds to a part only of the whole angular gyrus of the monkey. Cf. Fig. 125 with Fig. 129.) Some authors have, in accordance with this, put forward the theory that the occipital lobe serves as a cortical centre for the optic tract of its own side only, and so for one half of each retina, while in front of this on the angular gyrus is a centre in which both optic tracts are represented. But the clinical histories bearing on this point cannot be regarded as wholly satisfactory; and with reference to the experimental results we may once more insist, and the warning applies perhaps with particular force to these experiments on vision, on the danger of confounding those immediate effects of operative interference, which are of the nature of 'shock' in the wide sense of that word, with those pure 'deficiency' phenomena which are alone the outcome of the loss of the part removed. It is difficult to resist the conclusion that much of the transitory blindness which is observed in these experiments belongs to the former category, that the effect is transient because it is of the nature of shock and not because the loss of faculty is supplied by some other cortical area being subsequently substituted for the one removed. In the dog, injury to the frontal region of the cortex unaccompanied by any secondary mischief in the occipital region, has led to impaired vision; and this was probably an instance of 'shock,' for we have no other reason to connect the frontal region of the cortex with vision. We must be very careful in drawing the conclusion that, because an operation produces transient blindness, the part operated on has a direct share in vision; and we may well hesitate to accept the view that the whole retina is represented in the crossed hemisphere.

In conclusion we may say that, when all the many results which have been arrived at by experiment or by clinical observation are duly weighed, it will be felt that while the evidence for the occipital lobe, especially the cuneus, being concerned in the matter is convincing, we cannot in the present state of our knowledge, dogmatically exclude the angular gyrus, and that hence the only clear and consistent statement which can be made with any confidence is the broad and simple one that the hind region of the cortex is in some way intimately concerned in vision.

§ **673**. Such an attitude becomes all the more necessary when we ask ourselves the question what is it which actually takes place in the cortex during vision? Are we to conceive of it as if a visual impulse set going along the fibres of the optic tract underwent no essential change until it reached the cortex, as if it there suddenly developed into a 'visual sensation?' We can hardly suppose this. Between the cortex and the optic tract, the lower visual centres, the tegmental masses, intervene; and we can hardly suppose that interference with these bodies produces the same effect on vision as simple section of the optic tract. We have seen in a previous section that the frog and the bird certainly, and according to some observers also the rabbit, are in the absence of the cerebral hemispheres not totally blind, their movements being guided by retinal impressions; and cases are recorded of the dog being obviously still guided in some measure by retinal impressions after the occipital lobes had been wholly or almost wholly removed. And, though this is a matter at present outside exact knowledge, and though it is perhaps possible for simple afferent impulses to determine even complex movements without the intervention of 'consciousness,' we are probably justified in assuming that the simple visual impulses, travelling along the fibres of the optic tract, undergo important transformations in the tegmental masses, and that the changes which are propagated along the fibres of the optic radiation, constitute something quite different from the impulses along the optic tract or nerve.

Judging from the analogy of the motor region we may probably assume that in vision the cortical events are psychical in nature, and that the function of the optic radiation is to furnish what we may call crude visual sensations for further psychical elaboration.

Nor need this view compel us to suppose that injury to, or removal of the cortex must produce only psychical blindness or psychical impairment of vision, though this point has probably not been sufficiently held in view during the various experiments, sufficient care not having been taken to determine how far the blindness was purely psychical. Bearing in mind the degeneration following upon lesions of the occipital cortex, and the far-reaching effects of any operation on the brain, we may suppose that injury to the cortex affects the lower centres as well; and some of the transient impairment of vision, on which we have just dwelt, may perhaps be explained as the effect of the cortical injury on the lower centres.

Although the matter is thus in many of its details at present outside our exact knowledge, we may probably conclude that in the complex act of complete vision, while part, especially the more psychical part, is carried out in the cortex, more particularly of the occipital region, part is accomplished in the lower centres, the tegmental masses. As to the several functions of the three masses, we know almost absolutely nothing. Electric stimulation, and it is said, mechanical stimulation also, of the anterior corpora quadrigemina in mammals, or the optic lobes in lower animals calls forth movements of the eyes, and of various parts of the body; and removal of them causes blindness and in some cases loss of coordination of movements. Our knowledge on these points is not very exact; but from the above facts as well as from the connections of the anterior corpora quadrigemina with the parts of the brain behind we may possibly suppose that these bodies are more especially concerned with the part visual impulses play in determining the coordination of movements. We must remember, however, that all three masses are connected with the cortex, and probably all three play a part in vision even of the highest psychical kind.

Sensations of Smell.

§ **674**. The olfactory nerve, which is undoubtedly the nerve of smell, stands like the optic nerve apart from the rest of the cranial nerves; and a few words as to its structure and relations will be necessary.

Lying on the ventral surface of the anterior region of each hemisphere, on each side of the anterior fissure, is seen the olfactory bulb, which is prolonged directly backwards as the olfactory tract, coming apparently to an end where the hind margin of the frontal lobe abuts on the anterior perforated space in the floor of the front part of the third ventricle. The bundles of fibres forming the olfactory nerve proper spring from the bulb, which is their immediate cerebral origin, both bulb and tract being really parts of the cerebrum. Just as the fore-brain buds off on each side the optic vesicle to form the optic nerve, so each cerebral vesicle buds off an olfactory vesicle, the front part of which becomes the rounded bulb and the remainder the rounded trigonal tract or peduncle connecting the bulb with the hemisphere. In man the original cavity of the vesicle is obliterated, being filled up with neuroglial gelatinous substance, but in the lower animals remains as a linear space, the ventricle of the olfactory tract.

The bulb is a specialized mass of grey matter, forming a sort of cap to the end of the tract, and presents some analogies with the cortex of the hemisphere. Along the middle line lies the core of neuroglial gelatinous substance; but the side of the bulb dorsal to this core, in contact with the hemisphere, is much less developed than the side lying ventral to the core, next to the cribriform plate; and we may confine ourselves to the ventral portion. Next to the neuroglial core lies a layer of longitudinal medullated fibres, with which are mingled some nerve cells. This layer, which forms the beginning of the tract inside the bulb, is thinnest at the rounded front extremity of the bulb and gradually thickens backward. Next to it lies a 'nuclear' layer, composed of small nuclear cells, arranged to a large extent in longitudinally disposed rows. Fibres from the preceding layer pass between the groups, which are moreover separated by interlacing bundles of fibres. Next to this layer comes a somewhat thick one, which perhaps may be compared to the molecular layer of the cerebellum or to the pyramidal layers of the cerebrum. It is composed of a molecular ground substance, partly neuroglial in nature, traversed by numerous fibrils and fibres, many of the latter being of the fine medullated kind; it also contains, in no large number in man, nerve cells, some of which from their triangular form and tapering branched processes are not unlike the pyramidal cells of the cortex. The larger of these cells are generally found near the nuclear layer. Next to this molecular layer, or 'gelatinous layer' as it is sometimes called, comes, still working outwards towards the surface, a characteristic layer in which are found the 'olfactory glomeruli'; and outside this is the layer of olfactory fibres proper, that is to say, fibres non-medullated (§ 70) but bearing an obvious neurilemma. These olfactory fibres are arranged in a close set plexus, and bundles of fibres gathered up from the plexus at intervals pierce the pia mater, which invests the bulb and furnishes it with an ample supply of blood vessels, to form the olfactory nerve proper. The structure of the olfactory glomeruli, which are about ·05 mm. in diameter, has not yet been fully made out; they are described as being formed by coils of the olfactory fibres with small cells and blood vessels interspersed among the coils; in the lower animals a finely granular ground substance is present. Fibres from the layers beneath have been traced to them. We may perhaps assume that they serve as the immediate origin of the olfactory fibres; but their exact relations to the other layers of the bulb are by no means clear.

The tract is composed partly of longitudinal fibres, with which are mingled nerve cells, and partly of neuroglial gelatinous substance. The fibres begin in the bulb, which appears to serve as a relay between them and the fibres of the olfactory nerve proper; and while some appear to end in cells in the tract itself, others are continued on to the end of the tract, being joined by fibres taking origin along the tract. We may compare the bulb and the tract to a part of the retina (as we shall see, a part of the retina corresponds to the olfactory mucous membrane) and the optic nerve.

The dorsal surface of the tract is adherent to and continuous with the substance of the cerebral hemisphere, in a groove of which it lies, but the tract may be considered as independent of the hemisphere until it reaches its end, at which it breaks up into bands of fibres, spoken of as its 'roots.' The most conspicuous of these is a lateral one, which sweeping laterally across the anterior perforated space, at the mouth of the fissure of Sylvius, may be traced to the nucleus amygdalae (Fig. 116, *Na*), and the junction of this with the hippocampal or uncinate gyrus (Fig. 130) in the temporal lobe of the hemisphere of the same side. A much smaller median one, which however in some of the lower animals is large and conspicuous, takes a median direction, passes into the anterior commissure (§ 635) and so reaches the olfactory tract of the opposite side. Other small roots have also been described.

§ 675. In many animals in whom the sense of smell is acute, a portion of the cortex, known as the "pyriform lobe" or "hippocampal lobule," and which is anatomically continuous with the front end of the hippocampal gyrus (the part to which the name uncinate gyrus is often restricted), acquires relatively large dimensions. This and the anatomical relations just mentioned would lead us to suppose that a part of the cortex which is continuous with the front end of the hippocampal gyrus is in some way connected with smell. The argument from comparative anatomy, however, is one which must be used with caution; since, besides the great difficulty of determining the homologies of parts of the brain in different animals, relative increase in the part in question might be correlated to other things than the power of smell, and might be determined by circumstances having no relation to smell.

The experimental evidence, though on the whole it gives support to the view, is conflicting; and when the difficulty of determining whether a "dumb animal" can or cannot smell is borne in mind, this will not be wondered at. The observation that electrical stimulation of the region in question gives rise to movements of the nostrils, which have been interpreted as sniffing in response to subjective olfactory sensations, cannot have much weight; and while some observers have found that the removal of this part of the brain destroys the sense of smell, others have obtained negative results.

The few clinical histories which bear upon the matter are perhaps more trustworthy. These seem to shew that a lesion involving the cortex of this region, but leaving the olfactory bulb and tract, as well as other parts of the brain, intact, may destroy or greatly impair smell. And we may perhaps give particular weight to the cases in which epileptiform attacks, preceded by an 'aura' in the form of a peculiar smell, have been associated with disease limited to this region; for the phenomena of 'aura' seem to be connected with cortical processes.

Though the evidence on the whole goes to shew that the cortex at the front end of the hippocampal gyrus is especially connected with smell, and we have so marked it in Fig. 132, yet the whole matter stands on a somewhat different footing from the sense of sight. In man the relations of smell to the other operations of the brain (though, as we shall see in dealing with the senses, somewhat peculiar) are far more limited than are those of vision, and the psychical development of simple olfactory sensations is extremely scanty.

Sensations of Taste.

§ 676. This special sense though so closely associated with smell stands, together with the special sense of hearing, on a different footing from the two preceding special senses, since the nerves concerned belong to the category of ordinary cranial nerves, and we lack, in reference to them, the anatomical leading which is offered to us in the case of the optic and olfactory nerves.

We shall see in dealing with the senses that the fifth nerve and the glossopharyngeal nerve have been considered as nerves of taste, but that the matter is one subject to controversy; the gustatory function of the fifth is attributed to the peculiar chorda tympani nerve, and other questions have been raised. Whatever view we take, however, the nerves of taste are ordinary cranial nerves, and we have no anatomical guidance as to the fibres of either of the above two nerves making special connections with any part of the cortex. Though sensations of taste enter largely into the life of animals, and indeed of man himself, we have no satisfactory indications which will enable us to connect this special sense with any part of the cortex; the view indeed has been put forward that some part of the cortex in the lower portion of the temporal lobe, not far from the centre for smell, serves as a centre for taste; but the arguments in favour of this view are not, as yet at least, convincing.

Sensations of Hearing.

§ **677**. The cochlear division of the eighth or auditory nerve may be assumed to be a nerve of the special sense of hearing, and of that alone; the vestibular division serves, as we have seen, for other functions than those of hearing, § 642, but as we shall urge in dealing with the senses is not to be regarded as wholly useless for the purposes of that sense. The cochlear division we have traced, § 618, into the bulb, and the vestibular division into the lateral auditory nucleus (which perhaps may be regarded as a continuation or segmental repetition forwards of the cuneate nucleus or of part of that nucleus), and into the cerebellum, the cerebellar continuation being probably the part of the nerve which serves for coordinating functions. The connections of the auditory nerve with the cerebral hemisphere belong to the same category as those of other afferent cranial, and we may add spinal nerves; we have no very clear anatomical guide towards any particular part of the cortex.

When we turn to the empirical results furnished by experiment and clinical observations, we find that these, though even less definite and less accordant than in the case of the senses of sight and smell, point to part of the first or superior temporal (temporo-sphenoidal) convolution (Figs. 126, 129, 131) lying in the temporal lobe just ventral to the Sylvian fissure, as being specially concerned in hearing in some such way as the occipital lobe is concerned in vision.

Electrical stimulation of this region of the cortex gives rise to "pricking of the ears," and other movements such as are frequently connected with auditory sensations; but such phenomena are in this instance perhaps to be depended upon even less than in other similar instances. While some observers maintain that this convolution, the operation including other portions of the temporal lobe as well, may be removed from a monkey without producing any certain signs of deafness, other observers have found that removal of it on one side affected the hearing of the ear on the opposite side, and removal on both sides brought the animal into a condition in which, without being perhaps absolutely deaf, it reacted towards sound in a very imperfect manner indeed, very different from its normal behaviour. The scanty clinical histories bearing on this matter are not very decisive; for though deafness has been observed in connection with disease affecting the superior temporal convolution, the lesion has usually invaded other parts as well, and the deafness has been associated with other symptoms, notably aphasia. An auditory 'aura' has however at times been observed in connection with disease of this region, as also a peculiar psychical failure, known as "word deafness," in which, though sounds are heard, that is to say auditory sensations are felt, it may be even as usual, the perception or psychical appreciation of the sounds is lacking, and a spoken word is not recognized.

Lastly, we may add that, though as we said the anatomical leading is not definite, observers have found that, in new-born animals, on the one hand destruction of the part of the cortex probably corresponding to the region mentioned above, leads to atrophy of the median corpus geniculatum, and, to some extent of the posterior corpus quadrigeminum; and on the other hand destruction of the internal ear leads to an atrophy of part of the lateral fillet of the opposite crossed side which may be traced to the posterior corpus quadrigeminum, and thence to the median corpus geniculatum; and section of the lateral fillet on one side leads, among other results, to atrophy of the striae acusticae and tuberculum acusticum (§ 618) of the crossed side. This suggests that the path of auditory impulses is along the cochlear nerve to the lateral fillet of the crossed side, and so by the posterior corpus quadrigeminum and median corpus geniculatum to the cortex of the temporal lobe of that crossed side, the two later bodies bearing towards hearing a relation somewhat like that borne towards sight by the anterior corpus quadrigeminum and lateral corpus geniculatum. But the matter needs farther investigation.

There remains the special sense of touch, but this we had better consider in connection with sensations in general.

SEC. 9. ON THE DEVELOPMENT OF CUTANEOUS AND SOME OTHER SENSATIONS.

§ **678**. The sensations with which we have just dealt arise through impulses passing along special nerves or parts of special nerves, the optic nerve, the olfactory nerve &c.; we have now to deal with sensations arising through impulses along the nerves of the body generally. These are of several kinds. In the first place there are sensations which we may speak of as "cutaneous sensations," the impulses giving rise to which are started in the skin covering the body, or in the so-called mucous membrane lining certain passages. These sensations, which as we shall see in dealing with the senses are dependent on the existence of special terminal organs in or near the skin, are sensations of "touch," in the narrower meaning of that word, by which we appreciate contact with and pressure on the skin, and the sensations of "temperature," which again we may, as we shall see, divide into sensations of "heat" and sensations of "cold." These sensations may be excited in varying degree by impulses passing along any nerve branches of which are supplied to the skin. Then there are the sensations constituting the "muscular sense," to which we have already referred, and these again may be excited in any nerve having connections with the skeletal muscles.

As we shall see in dealing with the senses, when a nerve is laid bare and its fibres are stimulated directly either by pressure, such as pinching, or by heat, or by cold, or in other ways, the sensations which are caused do not enable us to appreciate whether the stimulation is one of contact or pressure, or of temperature, or of some other kind; we only experience a "feeling," which at all events when it reaches a certain intensity we speak of as "pain." And we have reason to think that at least from time to time impulses along various nerves give rise to sensations which have been spoken of as those of "general sensibility," by which in addition to other sensations, such as those of touch and of the muscular sense, we become aware of changes in the condition and circumstances of our body. When the stimulation of the skin exceeds a certain limit of intensity, the sense of touch or temperature is lost in, that is to say, is not appreciated as separate from the sense of pain; and under abnormal circumstances acute sensations of pain are started by changes in parts, for example tendons, the condition of which under normal circumstances we are not conscious of appreciating through any distinct sensations, though it may be that these parts do normally give rise to feeble impulses contributing to 'general sensibility.' It may therefore be debated whether 'pain' is a phase of all sensations, or of general sensibility alone, or a sensation sui generis. We shall have something further to say on this matter when we treat of the senses; meanwhile it will be convenient for present purposes if we consider that the sensations we have to deal with just now are the sensations of touch and of temperature, those of the muscular sense, and those of general sensibility including those of pain.

§ **679.** The fairly convincing evidence that the occipital cortex has special relations with vision, and the less clear evidence that other regions have special relations with smell and hearing, suggest that special parts of the cortex have special relations with the sensations now under consideration. But in the cases of the senses of sight and smell we had a distinct anatomical leading; and we have seen how uncertain is the evidence where such an anatomical leading fails, as in hearing and taste. In the case of sensations of the body at large, the anatomical leading similarly fails. Moreover any attempt to push the analogy of sight raises the following question. If there were two optic nerves on each side of the head, would there be two cortical areas, one for each nerve, in each hemisphere, or one visual area only? And again, if the optic nerve were the instrument for some sense in addition to that of sight, would there be two cortical areas, one for each sensation, or one area only serving as the cortical station so to speak of the whole nerve? If we push the analogy of sight it is open for us, since we cannot give a definite answer to the above question, to suppose either that there is one area for touch, another area for temperature, and so on, each for the whole body, or that there is an area for sensations of all kinds for each afferent nerve, or, that there is an intricate arrangement which supplies all the combinations of the two which are required for the life of the individual. Of the three hypotheses the latter is the more probable; but if so, it is by its very nature almost insusceptible of experimental proof, especially when we bear in mind what we have already said touching the difficulty of judging the sensations of animals. If the judgment of visual sensations is difficult, how much more difficult must be the judgment of sensations of touch and temperature? Indeed, sensations of pain are the only sensations of which we can form a quantitative judgment in animals; and our method of judging even these, namely, by studying the movements or other effects indirectly produced, is a most imperfect one.

We can learn therefore almost absolutely nothing in this matter from experimental stimulation of the cortex in animals. As we have previously (§ 671) urged, the absence of movements when parts of the cortex other than the motor region are stimulated is no evidence that the stimulation does not give rise to psychical events into which sensations enter; and movements follow stimulation of the motor area, not because that area is wholly given up to motor events, but because from the histological arrangement the stimulus gets ready access to relatively simple motor mechanisms. That the motor region has close connections with sensory factors is not only almost certain on theoretical grounds, but is shewn in many ways, for example by the experiment, described in § 661, of exalting the sensitiveness of a motor area by generating peripheral sensory impulses.

Nor can the effects on sensation of removal of parts of the cortex be interpreted with clearness and certainty. In the monkey removal or destruction of the gyrus fornicatus (Figs. 125, 127) on the mesial surface of the brain, ventral to the calloso-marginal sulcus which forms on the mesial surface the ventral limit of the motor region (an operation of very great difficulty), has brought the whole of the opposite side of the body to a condition which has been described as an anesthesia, that is a loss of all cutaneous tactile sensations, and an analgesia, that is a loss of sensations of pain, the condition being accompanied by little or no impairment of voluntary movements and, though apparently diminishing as time went on, lasting until the death of the animal some weeks afterwards. Again, removal of the continuation of the gyrus fornicatus into the gyrus hippocampi has in other instances led to a more transient anesthesia also of the whole or greater part of one side of the body. And it is asserted that removal of no other region of the cortex interferes with cutaneous and painful sensations in so striking and lasting a manner as does the removal of parts, or of the whole of this mesial region.

These results, however, do not accord with clinical experience, which, though scanty, seems as far as it goes to shew that in man, when mischief apparently limited to the cortex produces loss of sensations, it is the parietal lobe corresponding to the motor region which is affected; but there appears to be no record of any case of a cortical lesion affecting sensation without affecting movement. We have previously called attention to the fact that the temporary loss or impairment of movement which follows removal of an area is frequently, if not always, accompanied by an impairment of cutaneous sensations in the limb or part 'paralysed'; and side by side with this we may put the experience that in the human epileptiform attacks of cortical origin, the seizure is at times ushered in by peculiar sensations, called the 'aura,' in the part movements of which inaugurate the march of convulsive movements. But these things do not shew that the cortical area is the "seat of sensations," they rather illustrate what we said concerning the complexity of the chain of which the events in the cortical area are links, and the close tie between sensory factors and the characteristic elements of the motor region.

In the dog, while removal of almost any considerable portion of the cortex affects sensation, removal of parts in the frontal region producing perhaps less effect than removal of parts in other regions, the loss or impairment of sensation appears to be transient, though having a duration broadly proportionate to the extent of cortex removed; and when a very large portion of the cortex is removed, some imperfection appears to remain to the end. We have already referred to the case of a dog from which the greater part of both cerebral hemispheres had been removed, but which remained capable of carrying out most of the ordinary bodily movements, and that apparently in a voluntary manner; in this case the "blunting" of cutaneous sensations was perhaps more striking than the imperfection of movement. It will be worth while to consider the condition of this dog a little closely, on account of the light which it throws on the problem which we are now discussing.

Clinical experience shews that in man the integrity of the cerebral hemispheres, and of the connection of the hemispheres with the rest of the central nervous system, is essential to the full development of sensations; and that in this respect each hemisphere is related to the crossed side of the body. A very common form of paralysis or "stroke" is that due to a lesion of some part of one hemisphere (the exact position of the lesion need not concern us now), frequently caused by rupture of a blood vessel, in which the patient loses all power of voluntary movement and all sensations on the crossed side of his body (including the face); he is said to be suffering from hemiplegia, "one sided stroke." Not only do voluntary impulses fail to reach the muscles of the affected side, but sensory impulses, such as those which, started for instance in the skin, would under normal conditions lead to sensations of touch, of heat or cold, or of pain, fail to effect consciousness, when they originate on the affected side; the patient cannot on that side feel a rough surface, or a hot body, or the prick of a pin. For the sake of clearness we suppose the loss of movement and sensation to be complete, but it might of course be partial. Such a case shews we repeat that the integrity of the cerebral hemisphere, and of the connections of that hemisphere, we may say of the cortex of that hemisphere, with the other parts of the nervous system, is essential to the development of the sensations; but it does not prove that the cortex of the hemisphere is the "seat" of the sensations, it does not prove that the afferent, and sensory impulses started in the skin, undergo no material change until they reach the cortex and are then suddenly converted into sensations; it only proves that in the complex chain of events by which sensory impulses give rise to full conscious sensations, the events in the cortex furnish an indispensable link. And the phenomena of the dog in question on the one hand illustrate how complex the chain is, and on the other hand suggest that the completeness of the loss of sensation in the hemiplegic man is not a pure "deficiency" phenomenon, but is due to the lesion affecting the chain of events in some way or other besides merely removing the link furnished by means of the cortex. For as we previously urged, the dog in question, however curtailed its psychical life may have been, seemed to a casual observer to feel and move much as usual. Neglecting visual and auditory sensations with which we are not now dealing, it needed careful observation to ascertain that some of the animal's movements fell short, the failure being apparently due to the lack of adequately energetic coordinating sensory impulses; a stronger stimulus than usual had to be applied to the skin in order to call forth the usual movements and other tokens that the stimulus was "felt." As we have before urged, it is impossible to suppose that the mere stump of cerebrum left in this case could have taken on all the functions of the lost hemispheres; and making as we have previously done full allowance for the differentiation between man and dog, we must conclude that in the more general sensations with which we are now dealing, as with the more special visual sensations, the full development of a complete sensation is a complex act of more stages than one between the afferent impulse along the afferent nerve and the affection of consciousness which we subjectively recognise as 'the sensation;' the cortical events are only some among several. It follows that any analogy between the cortical events which play their part in a sensation and the cortical events which immediately precede the issue of impulses from the motor region along the fibres of the pyramidal load is misleading; the highly differentiated motor localisation does not justify us in concluding that there exists a similar topographical distribution of sensations.

§ **680**. We may now attack the problem in a different way, and instead of beginning with the cortex begin with afferent impulses started along afferent nerves from their peripheral endings, and attempt to trace them centralwards. And first we may call to mind what anatomical guidance we possess. (§ 569.)

We have seen that the fibres of posterior roots, the channels of afferent impulses, end in the spinal cord in at least two main ways. One set are continued on, not broken by any relays, as the median posterior tract, and by this tract representatives of all the spinal nerves are connected with the gracile nucleus in which, § 610, the median posterior column ends. The other fibres of a posterior root appear to end in the grey matter not far from their entrance; but from the grey matter there starts the cerebellar tract, which, though not conclusively proved to be, may be assumed to be an afferent tract. We may therefore probably suppose that afferent impulses along certain of the fibres of the posterior root make their way upwards along the cerebellar tract, and there are some reasons for regarding the vesicular cylinder and the cells which represent this where it is not conspicuous in the regions of the cord, as a relay between the two systems of fibres. There are also the more scattered fibres of the ascending antero-lateral tract (§ 567), which probably is also an afferent tract, and therefore probably also connected with the posterior roots; but as we have seen our knowledge of this tract is imperfect, though, if as some urge it ends in the restiform body, we may perhaps consider it as similar at least to the cerebellar tract, and treat the two as one.

Thus there seem to be at least two main recognised paths, in the form of tracts of fibres, for afferent impulses along the cord; one along the median posterior column, the other along the lateral column in the cerebellar tract. The latter passes straight up to the cerebellum by the restiform body, travelling along the same side of the cord; and any crossing of impulses passing along this tract must take place before they enter the tract; we have however no anatomical guidance for such a crossing. The other path, along the median posterior tract, comes to end in the gracile nucleus; it has indeed been urged that the gracile nucleus is thus connected chiefly with the lower limbs and lower part of the body, and that the analogous posterior root fibres from the upper limbs and neck pass similarly into the cuneate nucleus, or at least into the median division of that nucleus, but this cannot be considered as proved. Moreover both the posterior columns, median and external, bring to these nuclei fibres which have started from some relay in the grey matter lower down, and which are not fibres coming straight without any relay from the posterior roots; these however we cannot distinguish from each other in their course beyond the nuclei. From the gracile and cuneate nuclei the path onward is a double one, one broad, one narrow. The broad path, the one having most fibres and presumably carrying most impulses, leads to the cerebellum by the restiform body; and here the path, previously continued exclusively along the same side of the cord, becomes partly crossed though remaining partly uncrossed, the sensory decussation in the bulb being the crossed and the other fibres passing from the nuclei straight to the restiform body being the uncrossed one (§ 612); the uncrossed one we may perhaps look upon as really an upper part of the cerebellar tract. The narrow path is the fillet (§ 634), by which some of the fibres from the nuclei are continued on towards the cerebrum. This path is a crossed one, the crossing taking place in the sensory decussation, and it carries relatively few impulses, the chief increase in the size of the fillet as it passes onward being due to fibres coming from structures other than the gracile and cuneate nuclei.

Hence of the sensory impulses travelling along continuous tracts in the spinal cord, these tracts apparently keeping always to the same side, the great majority pass to the cerebellum; and of these again the greater number, all those along the cerebellar tract, and some of those passing through the gracile and cuneate nuclei remain uncrossed to the end. The only path by which all these impulses thus passing to the cerebellum can gain access to the cortex of the cerebrum, is by some or other of the ties between the cerebellum and the cerebral cortex. The relatively few impulses which pass along the fillet are for the most part landed in the middle parts of the brain, for only a small portion of the fillet passes to the cortex (§ 634), and it is not clear that this part of the fillet comes from the gracile and cuneate nuclei, so that most of these impulses can gain access to the cortex only by the relays of these middle parts of the brain.

Very striking indeed are these constant relays along the path of sensory impulses; in this respect the sensory impulses offer a strong contrast to the motor impulses. But a still more complex system of relays has to be mentioned; for yet a third path is open for sensory, afferent impulses along the cord. We must admit the possibility of afferent impulses travelling along the network of the grey matter, their path being either absolutely confined to the grey matter, or leaving the grey matter at intervals, and joining it again by means of those, longer or shorter, commissural or internuncial fibres which unite the longitudinal segments of grey matter, and form no inconsiderable portion of the whole white matter of the cord. We have seen (§ 586) that under abnormal circumstances, impulses pass freely in all directions along the grey matter, and we may conclude that under normal circumstances they can pass along it, under restrictions and along lines determined by physiological conditions. The fibres in the white matter which do not shew either descending or ascending degeneration are, probably, as we have said (§ 581), internuncial fibres, connecting segments of grey matter in a longitudinal direction; and, though we have no exact knowledge touching this matter, we may suppose that some of these convey impulses upwards, and others downwards.

If, as some maintain, the fibres of the ascending antero-lateral tract end not in the cerebellum, but in the grey matter of the bulb, or higher up, we have a fourth path for sensory impulses, which after the primary relay in the segmental grey matter pass straight up to the bulb.

§ 681. How do experimental results and clinical histories accord with such an anatomical programme?

We may first call attention to an experiment, which though somewhat old, carried out on rabbits, and confined to one region only of the cord, the lower thoracic, has nevertheless a certain value on account of its affording more or less distinctly quantitative and measurable results. We have seen, § 175, that afferent impulses started in afferent fibres, in those for instance of the sciatic nerve, so affect the vaso-motor centre in the bulb as to cause a rise of blood-pressure, at least in an animal under urari. Those afferent impulses must pass by some path or other from the roots which supply the sciatic nerves with afferent fibres along the thoracic and cervical cord to the bulb. If the path be blocked, the stimulation of the sciatic nerve will fail to produce the usual rise of blood-pressure. Now in a rabbit, the amount of rise of blood-pressure following upon the stimulation of one sciatic nerve with a certain strength of current having been ascertained, it is found that a much less rise of blood-pressure or none at all follows the same stimulation after division of certain parts of the cord in the mid or upper thoracic region; that is to say, the section of the cord has partially or completely blocked the path of the afferent impulses. Further, the block is conspicuous when the lateral column is divided, and is not increased by other parts of the cord being divided at the same time; when both lateral columns are divided the block is almost complete. And further, supposing one sciatic, say the right, is the one which is stimulated, a block occurs both when the lateral column of the same, right, side and when that of the crossed, left, side is divided, but is greater when the division is on the crossed than when it is on the same side. We may infer that the impulses, which reach the lumbar cord by the roots of the sciatic nerve, travel up the cord, or give rise within the lumbar cord to events which we may compare to nervous impulses, and which travel up the cord in such a manner that in the lower thoracic region they pass almost exclusively along the fibres of the lateral column, some having kept to the same side of the cord, but more having crossed over to the opposite side, before reaching the thoracic region.

This result was obtained in rabbits, and the experiment was carried out in the lower thoracic region only; the conclusions to be drawn from it hold good for that animal only, and for that part only of its cord. Moreover, the experiment only tests the path of such impulses as reach and affect the vaso-motor centre in the bulb. It is however exceedingly probable that the impulses which, generated in sensory nerves, affect the vaso-motor centre are impulses which, in the conscious animal, give rise to sensations of pain; in an intact animal changes in the vaso-motor centre occasioned by the stimulation of sensory nerves are accompanied by signs of more or less pain. And indeed this is confirmed by the fact that similar results were obtained when, the experiment being conducted in a similar way, signs of pain instead of variations in blood-pressure were taken as the tokens of the blocking of impulses. Hence, assuming this, we may regard the experiment as indicating that the impulses which form the basis of painful sensations pass by the lateral columns in the lower thoracic region of the cord of the rabbit, and therefore, though this is a further assumption, by the same columns along the whole length of the cord. We further may infer that while some of the impulses keep to the same side of the cord, others, and indeed the greater number, cross to the opposite side.

These conclusions entail assumptions, but the main interpretation of the whole experiment entails a still greater assumption. The testing of the influence of the sciatic stimulation was carried out soon after the section of the cord, and yet we have assumed that the block of the impulses was due to a pure deficiency phenomenon, the absence of a usual path. But we have no right to do this. It is possible that the section produced, in some way or other, a depressing or inhibitory effect lower down in the cord, affecting structures other than the lateral columns; all our experience indeed of the effects of operations on the cord would lead us to expect this. It is further possible that a section of the lateral column might produce this depressing effect, while sections of other parts did not, or might produce more effect than they could. It is possible for instance that the section of the thoracic lateral column inhibited, for the period during which the experiment was carried out, the grey matter of the lumbar cord and that the block really took place in this grey matter. Until the uncertainties thus attending the interpretation are removed the experiment is not valid as a proof that the lateral columns are the paths of afferent impulses; it would, however, still serve to indicate that the afferent impulses reaching the cord along the sciatic nerve crossed over to a large extent before they came under the influence of the inhibition, since we have no evidence to shew that such an inhibitory action of the section would be exerted chiefly on the crossed side.

Again, we have seen that the afferent impulses affecting the vaso-motor centre gain access to that centre without the help of the parts of the brain above the bulb; the existence of the vaso-motor centre was made out, § 176, by combining stimulation of a sciatic nerve with a series of operations consisting in making successive transverse sections of the bulb from above downwards; and it was not until the sections reached the vaso-motor centre that the blood-pressure effects of the sciatic stimulation were modified. Hence if the experiment be taken as shewing that not only afferent impulses affecting the vaso-motor centre, but other afferent impulses also travel by the lateral columns, it would also seem to shew that these other impulses pass in like manner to the bulb, and gain access to the cortex through the bulb. This increases a difficulty which presents itself even when the afferent impulses affecting the vaso-motor centre are alone considered. If the experiment means anything, it means that the impulses having in some way or other reached the lateral column, travel up that column by some continuous path, and indeed is generally taken as having that meaning. But if we put aside the very doubtful view that the ascending antero-lateral tract ends in the bulb, there is no continuous afferent tract in the lateral column ending in the bulb; the only definite continuous afferent tract in the lateral column of which we have any clear knowledge, namely the cerebellar tract, ends not in the bulb but in the cerebellum. And if we attempt to get out of the difficulty by supposing that those impulses at least which affect the vaso-motor centre, after travelling for some distance in the cerebellar tract, leave that tract for some path leading to the bulb (and the cerebellar tract does probably give off as well as receive fibres along its course), we practically admit that the experiment does not prove the existence of a continuous path.

A further difficulty is raised by the fact that, according to the interpretation which we are discussing, the section of the lateral column breaks the paths of what we may consider two kinds of impulses; those, the larger number, which have already crossed from one side of the cord to the other, and those which have remained on the same side. For, as we have already said, we have evidence, in man at least and some other animals, that afferent impulses cross completely over somewhere or other on their path before they are developed into full sensations; and we have also evidence, though less strong, that they cross not long after their entrance into the cord. But, if we suppose this to be the case in the rabbit also, it follows that in the experiment in question the impulses which were blocked on their passage along the lateral column of the same side, whatever the way by which they reached that lateral column, were pursuing a path which would eventually have led them to the other side of the cord. Hence the section of the lateral column, in breaking their path, broke not a continuous path keeping to the lateral column up the length of the cord, but a path which soon left the lateral column to pass elsewhere. The experiment therefore, as far as the impulses passing up the same side are concerned, does not prove that they pursue a continuous path along the lateral column; and if so what becomes of its validity of the experiment as regards the impulses crossing over from the other side, for the experiment in itself makes no distinction between the two?

We may add however that though the point has not been specially investigated, it is possible that in the rabbit, in whose hind limbs bilateral movements are so predominant, there is associated with the movements a bilateral arrangement for sensations, and that those impulses which remain along the same side of the cord as the nerve in which they originate, are carried up to the brain without any crossing at all.

§ 682. The results of this vaso-motor experiment then, though they are frequently quoted, do not when closely considered afford adequate proof that afferent impulses pursue a continuous path along the lateral columns of the cord, and moreover the facts brought to light by the experiment shew but little accord with the anatomical programme. We have dwelt on it so long because it is more or less illustrative of the many difficulties attending the interpretation of experiments of this kind; and it is in this respect all the more valuable because the actual experimental results are sharp and clear. We may pass over more rapidly the numerous experiments on the lower mammals, such as rabbits and dogs, in which other indications of sensation have been made use of, chiefly those which are the signs of painful sensations; these have been carried out in various regions of the cord, but chiefly in the thoracic region, and in them a like uncertainty of interpretation is farther increased by the want of exactness and agreement in the results.

If we content ourselves with making no distinction between the different kinds of afferent impulses, and in the case of these animals it would hardly be profitable to attempt to make a distinction, we may say that the several experiments so far agree that they point to the lateral columns as being the chief paths of afferent, sensory, impulses, or to speak more exactly, to the passage of these impulses being especially blocked by section of the lateral columns. Some observers find that in the dog and other lower mammals a section of the lateral column on one side, or at least a hemi-section of the cord, produces 'loss of sensation' on the opposite side greater than on the same side, or confined to the opposite side, and even accompanied by an exaltation of sensation, a hyperesthesia, on the same side. Other observers again, and these certainly competent observers, find that, in the dog, section of one side affects sensation on both sides, and indeed chiefly on the same side. We may perhaps once more repeat the warning how difficult is the quantitative and qualitative determination of sensations in such an animal as the dog; and may remark that in all these cases of unilateral section the increased blood supply due to failure of the normal vaso-constrictor tone must influence the peripheral development of sensory impulses.

In these experiments, as in those on voluntary movements, it is most important to distinguish between immediate or temporary and more lasting effects; and observers have found that the loss of sensation following a hemisection of the cord, like the loss of voluntary movement, is temporary only, and eventually disappears, though the recovery is slower and less complete than is the case with movements. As with voluntary movement (§ 663) so with sensation, recovery, though less complete than that of movement, is possible when a hemisection on one side has been at a later date followed by a hemisection on the other side. We may therefore repeat in reference to sensations the remarks which we then made in reference to movement; there is however an important difference between the two cases; in respect to movement we have evidence that under normal conditions the pyramidal tract plays an important part, and that any other path for volitional impulses is more or less an alternative one, whereas in respect to sensation we have no anatomical or other distinct proof of any such normal path.

The experiments on monkeys are in like manner neither accordant nor decisive; and even in these animals with their more varied signs of sensations, the interpretation of these signs is beset with fallacies. Some observers have found that a hemisection (in the thoracic region) produced loss of sensation on the crossed side, accompanied by little or no loss on the same side; other observers again have failed to obtain after a hemisection satisfactory proof of any such marked loss on the crossed side. Further, large portions of the lateral column, the more internal parts adjacent to the grey matter being left, have been removed without any very obvious and certainly without any lasting defects of sensation on the one side or on the other.

§ **683.** The clinical histories of diseases of the spinal cord in man bring to light in a fairly clear manner a fact of some importance, namely, that the several impulses which form the bases of the several kinds of sensations, of touch, heat, cold, and pain, and of the muscular sense, are transmitted along the cord in different ways and presumably by different structures. For disease may impair one of these sensations and leave the others intact. Thus cases of spinal disease are recorded, in which on one side of the body or in one limb ordinary tactile sensations seemed to be little impaired, and yet sensations of pain were absent; when a needle was thrust into the skin no pain was felt, though the patient was aware that the needle has been pressed upon the skin at a particular spot; and conversely in other cases pain has been felt upon the insertion of a needle, though mere contact with or pressure on the skin could not be appreciated. Again, cases are recorded in which the skin was sensitive to touch or pain, but not to variations of temperature; it is further stated that cases have been met with in which cold could be appreciated but not heat, and vice versa; and there are some facts which point to sensations of pain being more closely associated with those of heat, and tactile sensations with those of cold, than those of pain with those of touch or those of heat with those of cold. Cases of spinal disease are also recorded in which the muscular sense appeared to be affected apart from other sensations. We shall return to these matters later on in dealing with the senses; we refer to them now simply as shewing that disease, limited as far as can be ascertained to the spinal cord, may affect the several sensations separately, and therefore as suggesting that the several kinds of impulses, forming the bases of the several kinds of sensation, are transmitted in different ways and follow different "paths" along the spinal cord.

Clinical histories moreover agree, at least to large extent, in shewing that when the lesion is confined to one half of the cord, the sensations affected in the parts below the level of the lesion are chiefly or even exclusively those of the crossed side. But there is not entire accordance, especially as to the crossing being complete. And with regard to the muscular sense there is a distinct conflict of opinion; the majority of cases seem to shew that in unilateral disease or injury to the cord, the muscular sense in company with the voluntary movements, fails on the same side; but cases have been recorded in which the muscular sense in company with other sensations, seemed to be affected on the crossed side; it must be remembered however that it is very difficult to appreciate a deficiency of muscular sense mingled with deficiencies in other sensations, and we should à priori expect the muscular sense to run parallel with motor impulses.

When however we appeal to clinical histories or indications as to the several paths within the spinal cord taken by these several impulses, the answer is a most uncertain one, as indeed might be expected from the too often diffuse character of the lesions of disease; and it is perhaps not too much to say that no satisfactory deductions at all can be made.

§ **684**. Whether then we turn to experiments on animals or to the study of disease, the teachings with regard to sensation, in contrast to those with regard to voluntary movement, are in the highest degree uncertain and obscure. A few general reflections will perhaps help us to appreciate the value of such facts as we possess.

We have seen reason to think that in every movement whether voluntary and of cortical origin, or involuntary and started either as a simple spinal reflex or through the working of some part or other of the brain, the motor impulses, which sweep down the motor fibres to the muscles, issue marshalled and coordinated from the grey matter of the cord (for the sake of clearness we may omit the cranial nerves) from what we have called the motor mechanisms of the cord. Analogy would lead us to suppose that the afferent impulses, forming the bases of the several kinds of sensations, similarly left the afferent fibres to join the grey matter of the cord in what we may call the sensory mechanism. And such anatomical leading as we possess seems to support this view; with the exception of the median posterior tract, to which we will return immediately, all the fibres of a posterior root seem to end in the grey matter not very far from the entrance of the root. We have seen that a coordinate reflex movement may be carried out by at least a few segments of the cord; that a reflex movement may be started by stimuli of various kinds and therefore presumably by afferent impulses of various kinds; and that impulses forming the basis of the muscular sense are essential to the coordination of the movement. All our knowledge goes to shew that in a reflex movement carried out by a few segments of the cord, the whole chain of events between the arrival of the afferent impulses along the posterior root and the issue of efferent impulses along the anterior root may be carried out by grey matter, and grey matter alone. We may further infer that, while on the one hand the same procedure might obtain not through a few segments only but along the whole length of the cord, there would be an advantage, especially in respect to the rapidity of transmission, in employing internuncial tracts of fibres between the several segments, the advantage being greater the more distant the segments which have to work together.

We might further suppose that it would be of advantage to possess some direct path between the cerebral cortex and the spinal sensory mechanism immediately connected with the posterior root, such as is afforded by the pyramidal tract between the cortex and the spinal motor mechanism immediately connected with the anterior root. But no anatomical evidence of such a tract is forthcoming; and, as we have before remarked, along all the tracts which seem to be sensory in nature, in contrast to what takes place in the motor tracts, relays of grey matter are continually being interpolated.

The median posterior tract, since it gathers up representatives of successive nerves, presents itself as the nearest approach to such a sensory homologue of the pyramidal tract, though it ends in the bulb, and is not continued on directly to the cortex. And possibly it does play a somewhat analogous part, in so far as it serves as a special connection between the brain and the whole series of spinal nerves. But we are wholly ignorant as to what it really does; and whatever be the exact nature of the part which it plays, it probably has relations not to one kind of sensation only, but to all the different kinds of sensation. It has indeed been supposed by some to be especially a tract for the impulses of the muscular sense; but neither experiment nor clinical study affords adequate proof of this view. The condition known as locomotor ataxy, the salient feature of which is loss or impairment of muscular sense, is associated with disease of the posterior root and of its entrance into the cord, not with disease confined exclusively to the median posterior column. Moreover the tract cannot carry all the impulses of muscular sense, since some of them must pass at once into the grey matter, to take part in the coordination of reflex movements, and must therefore travel by fibres which do not form this tract. Similarly is there no adequate proof of the tract being an exclusive channel for tactile or for painful sensations.

We may also perhaps urge similar considerations with regard to the cerebellar tract, which though starting from a relay of grey matter is thence onward to the cerebellum a continuous tract. This tract also has been supposed to carry impulses of a particular kind, and more particularly those of muscular sense. There is less à priori objection to this view, since the tract starts from the grey matter, where the impulses of muscular sense may have already done their, so to speak, local work, and ends in the cerebellum, which as we have seen seems especially connected with the coordination of movements. But with respect to this tract also, neither experiment nor clinical study affords any clear and decisive proof that it is solely or even especially concerned with the muscular sense.

With regard to the antero-lateral ascending tract our knowledge is too imperfect to justify us in supposing that it is the special or exclusive channel for any one kind of sensation, or indeed in drawing any conclusions at all concerning it.

But when we subtract from the white matter of the cord these continuous tracts of ascending degeneration of presumably sensory or afferent function, and the continuous tracts of descending degeneration, which we may confidently speak of as motor or at least efferent, there are left only the fibres which we have (§ 581), supposed to be longitudinal commissural or internuncial fibres between successive segments. We are thus driven back to our former conclusion, that sensory impulses pass either by the grey matter alone, or by a series of steps as it were, by relays of grey matter connected by internuncial tracts of fibres, whose length we cannot ascertain, but which may be short. That such internuncial tracts intervene is rendered probable, on the one hand by the fact that section of the white matter, leaving the grey untouched, does affect sensations, and on the other hand by the fact that the several kinds of sensation appear to travel along the cord by separate paths, or at least may be separately blocked. It is of course, as we have already urged, possible that the effect of a section of a tract of fibres may be not the mere block due to loss of continuity, but some action on the grey matter with which the fibres are connected, whereby that grey matter fails of its usual functions and ceases to carry onward the sensory impulses reaching it from below; it is also possible that this or that lesion of disease may, directly or indirectly, affect particular parts of the grey matter or affect the grey matter in a particular way, so that a certain kind of sensory impulse, and none other is blocked. On the other hand we have reason to think that the rate at which impulses travel along the grey matter is very slow compared with that along nerve fibres; and in the struggle for life, rapidity of transmission of nervous impulses is of great importance. Hence the view that internuncial fibres intervene has more to commend it; it is moreover to a certain extent supported by clinical histories. But, if we accept this view, we must at the same time admit that, in animals at least, the lines provided by the internuncial tracts are not rigid, that within limits and under circumstances alternative routes are possible.

§ **685.** We may here perhaps raise once more, and this time more pointedly than before, the doubt whether we are justified in assuming, as we generally do assume, that the events which take place in the fibres connecting relays of grey matter within the central nervous system, are exactly the same as those which take place in the fibres of nerves outside the central system, during the passage of what we call a nervous impulse. Most of our knowledge of a nervous impulse has been gained by the study of the motor nerve of a muscle-nerve preparation. Our knowledge of the processes in afferent nerves is much more imperfect; but there are many facts which at least suggest that the molecular events constituting an afferent impulse along an afferent nerve are different from, and probably more complicated than, those constituting an efferent impulse along an efferent nerve. And, with regard to the processes taking place in fibres within the central nervous system we have hardly any exact experimental knowledge at all. It has been maintained by many observers that not only the grey matter but also the tracts of white matter in the spinal cord, while they are capable of conveying impulses in one direction or the other, are incapable of being so excited by artificial stimuli as to generate new impulses. These observers maintain that, when movements or signs of sensation follow the direct stimulation of various parts of the cord, the effects are due to issuing motor fibres or entering sensory fibres having been stimulated, and not to a stimulation of the intrinsic substance of the parts themselves; they propose accordingly to call these parts "kinesodic" and "æsthesodic" respectively, that is to say, serving as paths for motor or sensory impulses without being themselves either motor or sensory. The evidence on the whole goes to shew that this view is a mistaken one, that the various tracts of the spinal cord, like the pyramidal tract and indeed other parts of the brain, are excitable towards artificial stimuli. The question cannot, however, be considered as definitely closed; and the very fact that it has been raised illustrates the point on which we are now dwelling. We may further quote, in similar illustration of the same point, the following remarkable fact which was observed in the series of experiments referred to in § 663 on the effects of repeated hemisection of the spinal cord in dogs. The animal had partially recovered voluntary movements in his hind limbs after a third hemisection of the thoracic cord, and yet when, at his death, a strong tetanizing current was directed through the bulb and cervical cord, no movements of the hind limbs followed: the impulses started by artificial stimulation could not pass the bridge which sufficed for volitional impulses of natural origin. It is not too much to say that our experimental knowledge as to the events which accompany the activity of the structures within the central nervous system is almost entirely limited to the recognition of the "currents of action" referred to in § 657. We are already going beyond our tether when we assume on the strength of this that the processes started in the fibres of the pyramidal tract by artificial stimulation are in all respects identical with those started in the fibres of a motor nerve. We are going still more beyond our tether when we assume that the processes started in the same pyramidal fibres as the outcome of natural events in the motor cortex are of the same kind. But these assumptions are trifles compared with the assumption that the events taking place in the fibres of the optic radiation, passing from the pulvinar to the occipital cortex are identical with the events taking place in the fibres of the optic tract on the way to the pulvinar, or that the events travelling along the spinal cord to the brain as the result of a prick of the little finger are identical with those which the prick has started in the fibres of the ulnar nerve. Of the latter events we know a little; of the former events we know next to nothing. And we may here ask the question what is the meaning of these continual relays of grey matter along the sensory tract unless it be that at each relay, some transformation, some further elaboration of the impulses takes place, until what were the relatively, but only relatively, simple impulses along the fibres of the peripheral nerve are by successive steps changed in the complex events which we call a conscious sensation? This is what we had in mind, when we gave (§ 652) a note of warning concerning the danger of considering all the events in the central nervous system as either motor or sensory in nature. It is perhaps not an exaggeration to represent the views of some observers as if they supposed that afferent impulses, say tactile impulses, that is impulses eventually giving rise to tactile sensations, travelled unchanged from the skin to the cortex and there suddenly blossomed into sensations. If such a view were true, undoubtedly the chief task of physiology, almost the only one, would be to ascertain the tract along which these impulses passed. But if on the other hand the views just now urged have any real foundation, the question of tracts or paths sinks into insignificance compared with the almost untouched problems as to what are the several changes by which simple impulses are developed into full sensations, and when and how the changes are effected.

§ 686. Seeing how unsatisfactory is our present knowledge with regard to the tracts or paths of sensations in the relatively simple spinal cord, it would be useless to attempt any discussion as to their paths in the much more complex brain. If it be probable that the passage is effected by relays of grey matter in the former, the same method is much more probable in the latter; and if neither experiment nor clinical study throws much light on the path up to the bulb, these cannot be expected to give much help in the maze of grey matter and fibres by which the bulb is joined to the cortex. The several defined areas or collections of grey matter, and the several strands and tracts of fibres which we briefly described in a previous section, must have of course a meaning; but it may be doubted whether we have even so much as a correct glimpse of that meaning in any one case, if we except those which are in immediate connection with the cranial nerves and their nuclei. Seeing that the thalamus appears on the one hand to be connected with all or nearly all parts of the cortex, and on the other hand to serve as the front of the tegmental system, it is tempting to suppose that it plays an important part in sensations pertaining to the body generally, as part of it, the pulvinar, certainly does with reference to the special sense of sight; but we have no decisive indications as to what part it plays. And the part which it plays, whatever that may be, is not an exclusively sensory one, since both experimental and morbid lesions of the thalamus are apt to produce disorders of movement as well as other efferent effects. We ought perhaps to say the parts which it plays; for it is a complex body, having many ties and probably performing many duties.

The conspicuous fillet again, seeming as it does to be a special internuncial tract connecting what appear to be more particularly afferent or sensory parts of the bulb, such as the gracile and cuneate nuclei, with various parts of the middle brain and probably with the cortex, presents itself as a probable path of sensations of one kind or another from the body at large, the "narrow path" of the anatomical programme (§ 680); but in reference to this too, beyond its probable connection with the auditory sensations (§ 677), we lack evidence.

A conspicuous part of the brain, namely the cerebellum, naturally arrests our attention on account of its large connections with what appear to be afferent structures; in the anatomical programme, we called it "the broad path." By the cerebellar tract it has an uncrossed grip upon what is practically the whole length of the spinal cord; by the other constituents of the inferior peduncle it has a like uncrossed grip upon what appear to be afferent structures in the bulb, the gracile and cuneate nuclei, as well as on the eighth (vestibular) nerve and probably representatives of other afferent cranial nerves; it has further a crossed grip through the gracile and cuneate nuclei on the afferent posterior columns of the whole cord. It is of course possible that the cerebellar tract, though in itself uncrossed, lays its hand, by means of the vesicular cylinder for instance, on impulses which have already crossed from the posterior roots of the other side; for as we have seen the evidence as a whole shews that sensory impulses do cross over; but neither has the crossing of the impulses been definitely proved, nor has the path of the crossing been clearly demonstrated; while, on the contrary, the fibres of the auditory nerve which pass to the cerebellum, and which as we have suggested (§ 618), may be compared to an outlying part of the cerebellar tract, certainly continue uncrossed into the peduncle of the same side. We may conclude, therefore, that the ties of the cerebellum with the posterior roots are both crossed and uncrossed. And we may regard this double grip of the cerebellum on the cord, this grip on both sides of it, as an additional evidence that the ties of the cerebellum with the spinal cord are not merely for the purpose of serving as the channel for the impulses of muscular sense, but are the means by which the cerebellum transforms or elaborates sensory impulses, not of muscular sense alone or chiefly, but probably of all kinds, in order that they may take part in cerebral operations, of which the coordination of bodily movements may be one, but probably is only one of several or even of many.

SEC. 10. SOME OTHER ASPECTS OF THE FUNCTIONS OF THE BRAIN.

§ **687**. It is difficult to say anything definite concerning the transmission of sensory impulses and the development of sensations; it is still more difficult to say anything definite, beyond what has been already incidentally said, concerning the parts played in the work of the brain by the various aggregations of grey matter and tracts of fibres forming the middle part of the brain. Neither experiment nor clinical study has as yet afforded any clear or sure leading.

To what has already been said about the cerebellum, we may add the following.

Electrical stimulation of the surface of the cerebellum, in the monkey and in other animals, has led to movements of the eyes, and of other parts of the head; but we cannot from such results draw any satisfactory inferences.

The removal of various parts of the cerebellum, especially of the median parts, has led to a want of coordination in bodily movements; and an unsteady gait, due to a like want of adequate coordination, is a frequent symptom of cerebellar disease. But the incoordination which makes its appearance immediately after removal of, or injury to, the cerebellum may eventually disappear, even though large portions have been removed; and many cases of extensive cerebellar disease have been recorded in which the most perfect coordination of movements was retained. Hence the results of experimental and clinical study, while on the whole supporting the conclusion that the cerebellum has in some way to do with coordination, throw little or no light on the exact nature of the part which the organ plays in the complex process, but perhaps rather shew that we are at present wholly ignorant of how coordination is brought about.

Many hypotheses have been put forward as to the work carried out by the cerebellum, but none of these can be said to have an adequate basis. And, indeed, if there be any value in the reflections we have repeatedly made in previous pages, the physiologist ought not to use the words "functions of the cerebellum." From a physiological point of view it is, so to speak, a matter of accident, that various structures, the seats of various physiological processes, have, from morphological causes, been gathered together into the body which anatomists call the cerebellum. The task of the physiologist is to unravel the ties binding these various cerebellar structures with other parts of the central nervous system, and so with various parts of the body at large.

We must content ourselves here with calling attention to two or three broad and suggestive facts concerning its structure and connections.

In the first place, one striking fact about the cerebellum is the very large development of commissural fibres connecting together the superficial grey matter of the two hemispheres for the greater part of their extent, and passing, not only through the pons (§ 635) as part of the middle peduncle, but also through the median vermis. This great commissure is second only to the great callosal commissure of the cerebrum; and from the fact that median lesions of the cerebellum, those which do most damage to this commissure, are the most effective in causing incoordination and forced movements, we may infer that it in some way plays an important part in coordination.

A second striking fact is one on which we have already just dwelt, the connection, chiefly an uncrossed one, through the inferior peduncle, with the afferent structures of the bulb and spinal cord. We may now add, that the fibres of this peduncle passing into the centre of the white matter of the cerebellar hemisphere of the same side enclose the grey matter of the nucleus dentatus and appear largely to end in that body, though some pass on to the vermis.

A third striking fact is the connection, this being, as far as we know, wholly a crossed one, through the pons and pes, with the cerebral cortex, both of the extreme frontal region, and of the temporo-occipital region, and possibly or even probably with more scattered cortical elements of the parietal (motor) region. This connection is one between cortex and cortex, or at least between cerebral cortex and cerebellar superficial grey matter, for the fibres of the middle peduncle passing from the grey matter of the pons which serves as a relay end in the surface of the lateral hemisphere of the cerebellum. The frontal cortical fibres passing to the pes have a descending degeneration, that is from the cortex to the pons, and we may probably assume that the similar temporo-occipital fibres similarly degenerate downwards to the pons (§ 632). From this it has been inferred that this cerebro-cerebellar connection carries impulses from the cerebral cortex to the cerebellum; and it has been further inferred that these impulses are of the nature of motor impulses. As we have more than once urged, the character of degeneration, that is whether "ascending" or "descending" is not a satisfactory proof of the direction taken by impulses; but it is perhaps of more importance to remember that, as we have also urged, we have no right to assume that the impulses passing along such a tract as the one in question must be either sensory or motor, or indeed that such a tract serves as an instrument for producing effects in one direction only.

That during life the fibres of which we are speaking serve as an important chain by which cerebral cortex and cerebellum affect the one the other, there can be but little doubt; but we are wholly in the dark as to what really takes place along the fibres. We have seen (§ 593) reason to think that the brain may and does exert an inhibitory influence over the spinal cord; and the mechanical certainty with which an animal deprived of its cerebral hemispheres responds to stimuli, in contrast to the uncertainty attending the result of stimuli applied to an intact animal, as well as all the experience of our own daily life shews that the cerebral cortex can work in an inhibitory manner on other parts of the brain; the remarkable "forced movements" on which we dwelt in a previous section seem in some instances to be the result of the abrupt snap of some inhibitory bond. Conversely all the experience of our daily life, many of the phenomena of the condition known as hypnotism and of allied conditions, as well as various experimental results such as that quoted in § 661, where a sensory impulse seems to inhibit the activity of a motor area, shew that the cortex may itself in turn be inhibited by other parts of the central nervous system. But we have at present no satisfactory indications as to the paths of inhibitory impulses or as to how inhibition is brought about; nor have we any proof that the cerebro-cerebellar tract is an inhibitory one in either direction.

We may add that some of the fibres of the middle peduncle appear to be neither commissural nor connected with the cortical fibres in the pes, but to end in other ways; and tracts have been described as continuing onwards some of the cerebellar fibres of the middle peduncle on the one hand upwards toward the cerebrum, and on the other hand downwards towards the spinal cord. It has been further urged that these tracts are efferent in function.

Lastly, we may call attention to the superior peduncles. These, which as we have seen appear to come largely from the grey matter of the nucleus dentatus and to end in the tegmentum, largely in the red nucleus, may be regarded as constituting through the relay of the front part of the tegmentum another tie, presumably of a different nature from the foregoing, between the cerebellum and the cortex; indeed it used to be called the processus a cerebello ad cerebrum. It is an obviously crossed tract (Fig. 113, *SP*); it connects one nucleus dentatus, and so presumably by that relay the fibres of the inferior peduncle ending in that body, and perhaps other fibres proceeding from the superficial grey matter of one side of the cerebellum, with the red nucleus and other parts of the tegmentum of the crossed side, and thus with the cortex of the crossed side. It has been supposed that the direction of impulses passing along it is from the cerebrum to the cerebellum, but we have no clear proof of this; indeed as to what it does, we have no satisfactory evidence either experimental or clinical.

We may here incidentally remark that, in consequence of afferent tracts being traced to or towards the tegmentum and of the sharp contrast presented between the tegmentum and the conspicuously motor pyramidal tract in the pes, the view has gained ground that the tegmentum is essentially a sensory structure. But there does not appear to be adequate evidence either clinical or experimental for such a conclusion. The thalamus, which we have regarded as the front so to speak of the tegmentum, cannot, as we have already urged (§ 686), be considered exclusively or especially sensory. And many of the ties of the tegmentum, such as the fibres from the corpora striata ending in the substantia nigra, for this may be considered as properly belonging to the tegmentum, are of the kind which we may suppose to be efferent or motor. Indeed we may probably regard the whole tegmentum as being broadly the analogue in the forward segments of the cerebro-spinal axis of both the anterior and posterior grey matter of the spinal segments behind.

Though we are thus in the dark concerning what goes on in the cerebellum, it may be worth while to call attention once more to the remarkable characters of the superficial grey matter (§ 648). The many points of resemblance between it and the cerebral cortex cannot but suggest that the processes taking place in it have some analogies with cortical events. And it is at least a fact of some significance that congenital deficiency, or atrophy of the cerebral hemisphere of one side, is frequently accompanied by a corresponding deficiency of the crossed cerebellar hemisphere.

§ 688. Both the anterior and posterior corpora quadrigemina are complex in structure; not only do they differ from each other, but also in each the grey matter differs in different parts, both as to its nature and appearance and as to its connections with tracts of fibres. If we have little right to speak of the "functions of the cerebellum," we have even less right to speak of the "functions of the corpora quadrigemina" or of either pair of them. The anterior pair, as we have seen, has to do in some way with vision; but we have reason to think that a part only of the whole body is thus concerned; and there is some foundation for the view that of this part, one portion belongs, so to speak, to the optic tract and another portion to the cortical fibres of the optic radiation. Possibly still another part is concerned in bringing, as we have (§ 673) suggested, visual impulses to bear on the coordination of movements.

Stimulation of the surface of the posterior pair, besides giving rise to movements of various parts of the body, has in monkeys and some other animals, the singular effect of producing a vocal utterance in the form of a cry or bark. But we cannot make much use of these results for the purpose of drawing conclusions as to what share these bodies take in the whole work of the brain. In the frog, the optic lobes correspond to the two pair of corpora quadrigemina together; and the cry just mentioned may perhaps be put side by side with the fact that in the frog the optic lobes seem to furnish a mechanism for croaking; when the optic lobes are destroyed, the reflex croaking mentioned in § 638 is done away with. The probable connection of the posterior corpora quadrigemina with hearing is also interesting in this connection; but we have no satisfactory evidence of any special ties between the bodies in question and either the cortical area for phonation or the vocal mechanism in general; the occurrence of the cry remains so far an isolated fact.

In frogs, in which the cerebellum is very small, the optic lobes seem to be particularly concerned in the coordination of movements. When the brain is removed by means of a section behind the optic lobes the animal loses the power of balancing itself (§ 638), which it possesses when the section passes in front of the optic lobes; and injury to the optic lobes produces incoordination of movement and often "forced movements." It has been maintained that the loss of coordination is in these cases due to removal of or injury to the central grey matter in the walls of the third ventricle, and not to mere removal of or injury to the optic lobes; but the whole evidence goes to shew that in the frog and in the bird the optic lobes do play a part in the coordination of movement, though lesions of the central grey matter around the third ventricle, or indeed of the thalamus or other parts of the tegmentum, may give rise to loss of coordination or to "forced movements."

In the mammal removal of or injury to the posterior corpora quadrigemina does not cause blindness, but may, like a lesion of the anterior pair, give rise to loss of coordination or to forced movements; the effect, however, is in most instances very temporary. The connection of the anterior pair with vision suggests a clue as to how this pair takes part in coordination; but as to how the posterior pair could intervene in the matter we have hardly so much as a hint; for, even if we admit a connection between them and the sense of hearing, and, remembering that a loud sound will often cause a person to reel, further admit that purely auditory impulses, as distinct from what we have called ampullar impulses, may take part in the general coordination of bodily movements and in the maintenance of equilibrium, as they certainly do in the special coordination of laryngeal movements, still we are not much nearer an understanding of the matter. We may add that section of the lateral fillet, which appears as a conspicuous tie between the posterior corpora quadrigemina and the parts of the nervous system behind them, does not appear to have any marked effect in producing incoordination.

In fine, beyond the broad facts on which we dwelt in a previous section, namely, that we maintain our equilibrium and carry out complex movements involving often several parts of our body, through what we call coordination, that afferent impulses supply important factors of this coordination, and that the cerebellum, through the vestibular nerves in part at all events, together with other portions of the middle brain, are in some way its chief instruments, we as yet know very little. We have certainly no adequate knowledge as to how either pair of corpora quadrigemina exactly intervene in the matter, or, indeed, as to what other parts they play in the general work of the brain.

With regard to other tracts of fibres or areas of grey matter we have nothing to say, except as regards those which are more or less immediately connected with certain of the cranial nerves, such for instance as the nerves for movements of the eyes, and these it will be best to consider when we have to deal with the nerves themselves.

§ **689.** Besides the somatic functions which in previous discussions we have chiefly had in view, the brain as a whole undoubtedly carries out splanchnic functions; concerning these, however, we must be very brief.

Of the respiratory and vaso-motor functions of the bulb we have already treated in their appropriate places, and we have referred (§ 535) to the experimental evidence that a lesion of the corpus striatum, or of the front part of the optic thalamus has a remarkable influence on the development of heat in the body. We have further seen that the higher parts of the brain, acting through the bulb, exercise powerful influences on respiration, on the vaso-motor system, and on the beat of the heart. Daily experience affords abundant instances of actions such as these, as well as of the influence of the brain on other organic functions. We can bring our will to bear on the mechanism of micturition (§ 430) which is almost wholly, and on the mechanism of defæcation (§ 275) which is largely, splanchnic in nature. These movements, however, are not skilled movements; and as we explained in dealing with them, the action of the brain as regards them seems limited to augmenting or inhibiting the activity of spinal centres. We should therefore hardly expect them to be specially represented in the cortical motor region. But emotions have a much wider and more powerful influence over the splanchnic functions than has the will, and have the power of affecting the work of certain organs, for instance the heart and secreting glands, which the will is unable to touch. And since we have every reason to believe that the cortex is closely associated with the emotions, we may naturally infer that elements of the cortex supply a link in the chain through which an emotion influences this or that splanchnic activity; we may, accordingly, expect to find that stimulation of some part or other of the cortex produces splanchnic effects. The results of experimental investigation, however, are both scanty and discordant; but the greater weight should perhaps be attached to the positive results. Thus, some observers find that stimulation of the cortex, the locality being in the dog some part of the sigmoid gyrus, produces movements of the bladder; and they trace the path of this influence through the front part of the thalamus and the tegmentum to the bulb and so to the cord, excluding the cerebellum, which other observers believed to be concerned in the matter. Some observers again find that stimulation of the cortex produces a flow of 'chorda saliva,' while others maintain that the secretion, when it does occur, is an indirect and not a direct effect of the cortical stimulation; and it may be remarked that the cortical area, which is claimed to be a "salivation area," lying in the dog on the convolutions dorsal to and in front of the Sylvian fissure, is not either the area connected with the facial nerve, or that allotted to taste or smell.

Similarly, stimulation of parts of the cortex has in the hands of various observers led to movements or to arrest of movements of the intestines, to changes in the beat of the heart, and to various vaso-motor and other effects; but it will not be profitable to enter into any further details. We may, however, add the remark that when the cortical motor area for a limb is removed, or suffers a lesion, the temporary paralysis which is thereby caused is accompanied by a rise of temperature in the limb; this may be at times very great indeed; in the monkey for instance, the hand or foot on the paralysed side may be as much as 10° C. higher than that of the other side. The effect is partly due to vaso-motor paralysis, but, especially considering that the muscles of the limb are relatively quiescent and so producing less heat than usual, cannot be due to that alone. The remarkable result may be taken as still further illustrating the complexity of the processes connected with the cortical motor area; the area is in some way associated with the vascular arrangements and nutrition of the muscles with whose movements it is concerned.

§ **690**. There remain yet a few words to be said about the cortex. We regard, and justly so, the spontaneous intrinsic activity of the brain as the most striking feature of its life. The nearest approach to it which we find elsewhere in the body, is perhaps the rhythmic beat of the heart. The analogy between the "regular automatism" of the one, and the "irregular automatism" of the other is a striking one; and indeed our knowledge of the relatively simple spontaneity of the heart has probably influenced to a large extent our conceptions of the complex spontaneity of the brain. In the heart the rhythmic discharge of energy is chiefly determined by intrinsic chemical changes, by the metabolism of the cardiac substance; the influence of external circumstances, apart from those which provide an adequate supply of proper blood, is wholly subsidiary and serves only to raise or to lower the intrinsic changes from time to time, as occasion may demand. And the analogy of the heart has perhaps led us to exaggerate the part played in the brain by the like intrinsic chemical metabolism. (We are here of course viewing the action of the brain from the only stand-point admissible in these pages, the purely physiological one; but such a mode of treatment does not prejudge other points of view.) Some writers use expressions which seem to imply the conception that the nervous changes forming the basis of the psychical and other processes of the brain are chiefly the direct outcome of the chemical metabolism of the grey matter and especially of the nerve cells. They speak of "the discharge of energy" from these cells in the same way that we can speak of the discharge of energy from a cardiac fibre. But, to say nothing of the low rate of nervous metabolism as measured in terms of chemical energy, we have no experimental or other evidence of nervous substance in any part of the body being, like the cardiac substance, the seat of an important metabolism carried on irrespective of influences other than purely nutritive ones. In the case of nerve cells interpolated along nerves composed of fibres of the same kind, as in the sporadic ganglia, all the instances where the nerve cells were supposed to initiate active processes have, on examination, broken down; as we have seen, the ganglia of the heart do not supply the moving cause of the heart beat. It is only in the central nervous system where nerve cells, as part of grey matter, are found at the meeting of nerve-fibres of different kinds, that we have any evidence of "discharge of energy" from the cells.

As we pointed out (§ 597) in speaking of the spinal cord, the discharge of efferent impulses from the central nervous system, though it undoubtedly must have a certain chemical basis, namely the metabolism of the nervous substance, is, in the first line, dependent on the advent of afferent impulses. But this, if true of the spinal cord, is still more true of the brain, which receives or may receive not only all the impulses which reach it through the cord, but especially potent and varied impulses directly through the cranial nerves. All life long the never ceasing changes of the external world continually break as waves on the peripheral endings of the afferent nerves, all life-long nervous impulses, now more now fewer, are continually sweeping inwards towards the centre; and the nervous metabolism, which is the basis of nervous action, must be at least as largely dependent on these influences from without, as on the mere chemical supply furnished by the blood.

We have developed this point because of the influence it must have on our conceptions of the physiological processes taking place in the cortex. If we accept the view just laid down, we must regard the supereminent activity of the cortex and the characters of the processes taking place in it as due not so much to the intrinsic chemical nature of the nervous substance which is built up into the cortical grey matter as to the fact that impulses are continually streaming into it from all parts of the body, that almost all influences brought to bear on the body make themselves felt by it. To put the matter in a bald way we may ask the question, what would happen in the cortex if, its ordinary nutritive supply remaining as before, it were cut adrift from afferent impulses of all kinds? We can hardly doubt but that volitional and other psychical processes would soon come to a standstill and consciousness vanish. This is indeed roughly indicated by the remarkable case of a patient, whose almost only communication with the external world was by means of one eye, he being blind of the other eye, deaf of both ears, and suffering from general anesthesia. Whenever the sound eye was closed, he went to sleep. It is further indirectly illustrated by the following experimental result. We have seen (§ 654) that a vertical incision carried through the depth of the grey matter around an area does not prevent stimulation of the surface of the area producing the usual movements. But after such an incision the animal suffers a paralysis of the movements connected with the area, like that resulting from the removal of the grey matter of the area; and the operation is said to be followed by degenerative changes in the area, and degeneration of the pyramidal fibres starting from it. Some of this effect may be due to nutritive changes brought about by injury to the pia mater and division of blood vessels; but it cannot be wholly accounted for in this way; it appears as if the life of the area is curtailed when its nervous ties are broken.

We may conclude then that we are not justified in speaking of consciousness or volition, or other psychical processes, even admitting that these fail when the cortex is removed, as being functions of the cortex in the same way that we speak of the functions of other organs; they are rather functions of the connections of the cortex with the other parts of the central nervous system.

We should add that they are also functions of the connections of the several parts of the cortex with each other. All our knowledge goes to shew that psychical processes are dependent on, or are in some way associated with the cortex; but whatever classification of psychical functions we adopt, we are wholly unable to make out any localisation of functions, such as we can make out for movements, visual sensations and the like. Even taking the broad and elementary division into "the emotions" and "the intellect," we cannot satisfactorily allot either division to any particular part of the hemisphere. In dogs, removal of particular parts of the hemispheres has indeed been observed to change the character of the animal, converting for instance a vicious, morose dog into a mild and inoffensive one; and removal of the front parts of the hemisphere seems to have frequently a marked effect in rendering the animal more impressionable and excitable; he becomes much more demonstrative and 'gushing' in his behaviour than before. But these are mere hints, and the clinical histories of disease in man do not enable us to say much more. Such knowledge as we do possess rather tends to shew that the psychical processes in proportion as they become more complex involve a greater number of nervous factors, and therefore have for their material basis a greater width of nervous area, or in other words their localisation becomes less definite. Thus while we may localize the beginning of a psychical process, a visual sensation for instance, and one of its terminal acts such as the issue of impulses along the pyramidal tract, we cannot put our finger on the seat of the intermediate transactions. These even in the simplest processes must be complex, and must involve many factors. Our simplest conceptions of the external world are based on a combination of visual sensations and tactile sensations. It being granted that the visual sensation, in one phase of its development, is connected with certain changes in some spot of the occipital cortex, there must be some tie between this and the corresponding nervous seat of the tactile sensation wherever that may be, and further ties between these and other parts of the cortex. Hence as we said the psychical process is a function of connections.

Many of these ties are most probably furnished by the association fibres passing from one part of the cortex to a neighbouring part. We must also probably admit that impulses or to use a more general word, processes, may travel laterally along the tangle of the cortical grey matter, for this, like the grey matter of the spinal cord, seems to form a physiological continuity, no more broken by the fissures than is the cord by its segmental arrangement; and we know nothing as to the limits which must be placed on the distance to which such processes may travel from their focus of origin. Further, seeing how completely in the dark we are as to the reason why we possess two hemispheres, and especially seeing that, as shewn by speech, the whole of each hemisphere is not identical in action with the whole of the other, we may perhaps suppose that the fibres of the corpus callosum, which form so large a part of the central white matter of the hemisphere, have other duties than that of merely keeping the points of one hemisphere in touch with the corresponding points of the other hemisphere. But, when we have made every allowance for all these direct intercortical connections, we are driven to the conclusion that the indirect ties between one part of the cortex and another through the lower parts of the brain are of no less, perhaps of greater importance. This indeed is shewn by the relations of the motor region. We have already urged, that even as regards the mere carrying out of a skilled movement (and we may add whether that be voluntary or involuntary in the ordinary, common use of the words) the motor region must have other ties with the part moved than merely the efferent tie of the pyramidal fibres; it must have sensory afferent ties, and the course of these, including even perhaps those which belong to the muscular sense, we may regard as an indirect one along the spinal cord and middle parts of the brain, though the details are as yet unknown to us. It must moreover, as we have also seen, have ties, at least in many cases, with parts other than the part moved, for instance with the general coordinating machinery. And the ease with which some, not very obvious, change, will permit the stimulation of a limited motor area to start epileptiform convulsions, shews how many and close are the ties in another direction. Further, when we go beyond the final phases of the process in the motor cortex, to those which precede the issue of the efferent impulses, we find the ties multiplying. For instance, since our movements are so largely guided by visual sensations, there must be ties between the motor cortex and the central visual apparatus, it may be of the occipital cortex, but it may also be of the lower visual centres. As we insisted, the motor area is only a link in a complex chain; and what we can see, dimly though it be, in reference to the cortical motor processes, probably holds good for those other cortical processes as well, of whose nervous genesis we know at present nothing. Hence even the higher psychical events cannot truly be spoken of as functions of the cortex, meaning that they are simply the outcome of molecular changes in the cortical grey matter; they are rather to be regarded as the outcome of complex processes in which the parts of the brain below the cortex play a part no less important than that of the cortex itself. If so, the fibres passing down from the cortex to the middle brain have functions by which they take part even in our psychical life, functions for which neither the words motor nor sensory are fitting.

SEC. 11. ON THE TIME TAKEN UP BY CEREBRAL OPERATIONS.

§ **691**. We have already seen (§ 594) that a considerable time is taken up in a purely reflex act, such as that of winking, though this is perhaps the most rapid form of reflex movement. When the movement which is executed in response to a stimulus involves cerebral operations a still longer time is needed; and the interval between the application of the stimulus and the commencement of the muscular contraction varies according to the nature of the mental labour involved.

The simplest case is that in which a person makes a signal immediately that he perceives a stimulus, *ex. gr.* closes or opens a galvanic circuit the moment that he feels an induction shock applied to the skin, or sees a flash of light, or hears a sound. By arrangements similar to those employed in measuring the velocity of nervous impulses, the moment of the application of the stimulus and the moment of the making of the signal are both recorded on the same travelling surface, and the interval between them is carefully measured. This interval, which has been called 'the reaction period' or 'reaction time,' may be divided into three stages: (1) The time during which afferent impulses are generated in the peripheral sense organs and transmitted along the afferent nerves to the central nervous system; this may be called the "afferent stage." (2) The time during which, through the operations of the central nervous system, the afferent impulses are transformed into efferent impulses; this may be called the "central stage." (3) The time taken up by the passage of the efferent impulses along the efferent nerves and the transformation of the nervous impulses into muscular contractions; this may be called the "efferent stage." In the efferent stage the events are comparatively simple, and though not absolutely constant, do not vary largely; we are able to form a fairly satisfactory estimate of its duration and so of the share in the whole reaction period which may be allotted to it. The events of the afferent stage are much more complex and the estimates of its duration, being arrived at in an indirect manner, and chiefly based upon calculations of the whole reaction time, are very uncertain. Hence all attempts to estimate the length of the "central" stage, the "reduced reaction period" as it is sometimes called, by subtracting the efferent and afferent stages, must be subject to much error. But a good deal may be learnt by studying the variations under different circumstances of the reaction period as a whole.

Taking first of all the cases in which the events of the central stage are simple, such as those where the subject has merely to make a signal upon feeling a sensation, we find that the length of the reaction period is dependent on the intensity of the stimulus, being shorter with the stronger stimulus. But variations in the strength of the stimulus, especially in the case of minimal stimuli, have a much more striking effect in determining the certainty of the reaction than in affecting the length of the period. Thus when the signal is made in response to some visual sensation, upon seeing an electric spark for instance, if the spark be a very weak one the subject of the experiment often fails to make the signal at all, though he may rarely fail if the spark be a strong one.

Some of the most marked variations in the length of the reaction period are determined by the individuality of the subject. Thus with the same stimulus applied under the same circumstances the reaction period of one person will be found very different from that of another.

The length of the reaction period varies also according to the nature and disposition of the peripheral organs stimulated. In general it may be said that cutaneous sensations produced by the stimulus of an electric shock applied to the skin (the signal for instance being made by the right hand when the shock is felt by the left hand) are followed by a shorter reaction period than are auditory sensations, while the period of these is in turn shorter than that of visual sensations produced by luminous objects; on the other hand, the shortest period of all is said to be that of visual sensations produced by direct electrical stimulation of the retina. Roughly speaking we may say that the reaction period is for cutaneous sensations $\frac{1}{7}$th, for hearing $\frac{1}{6}$th, and for sight $\frac{1}{5}$th of a second.

Practice materially shortens the reaction period; indeed, after long practice, making the signal, at first a distinct effort of the will, takes on the characters of a reflex act, with a correspondingly shortened interval. Lastly, we may add that in the same individual and with the same stimulus, the length of the period will vary according to circumstances, such as the time of year, the weather, and the like, as well as according to the condition of the individual, whether fresh or fatigued, fasting or replete, having taken more or less alcohol, and the like.

The reaction period of vision has long been known to astronomers. It was early found that when two observers were watching the appearance of the same star, a considerable discrepancy existed between their respective reaction periods, and that the difference, forming the basis of the so-called 'personal equation,' varied from time to time according to the personal conditions of the observers.

§ **692**. The events taking place in the central stage are of course complex, and this stage may be subdivided into several stages. Without attempting to enter into psychological questions, we may at least recognize certain elementary distinctions. The afferent impulses started by the stimulus, whatever be their nature, when they reach the central nervous system undergo changes, and as we have seen, probably complex changes before they become sensations; and further changes, now of a more distinctly psychical character, are necessary before the mind can duly appreciate the characters of these sensations and act accordingly. Then come the psychical processes through which these appreciated sensations, or perceptions, or apperceptions as they are sometimes called, determine an act of volition. Lastly, there are the executive processes of volition, the processes which, psychical to begin with, end in the issue of coordinate motor impulses, or, in other words, start the distinctly physiological processes of the efferent stage. We may thus speak of the time required for the perception of the stimulation, of the time required for the action of the will, and of the time required for the complex psychical processes which link these two together. Accepting this elementary analysis, it is obvious that the total length of the central stage may be varied by differences in the length of each of these parts; and a more complete analysis would of course open the way for further distinctions. Hence, by studying the variations of the whole reaction time under varying forms of psychical activity, we may form an estimate of time taken up by various psychical processes.

We may take as an instance the case in which the subject of the experiment has to exercise discrimination. The mode of making the signal being the same, and the stimulus being of the same order in each trial, that is to say, visual, or cutaneous, or auditory, &c., and general circumstances remaining the same, two different stimuli are employed, and the subject is required to make a signal in response to the one stimulus, but not to the other; the subject has to discriminate between the psychical effects of the two stimuli. Suppose, for example, the stimulus is the sound of a spoken or sung vowel, and the subject is required to make a signal when *a* is spoken or sung, but not when *o* is spoken or sung. If the subject's whole reaction period be determined (i) in the usual way, with either *a* or *o* spoken (and the result will be found not to differ materially whether *a* or *o* be used), the subject knowing that only *a* or only *o* will be spoken, and then be determined again (ii) when he has to discriminate in order that he may make the signal when *a* is spoken but not when *o* is spoken, he not knowing which is about to be spoken, the whole reaction period will be found to be distinctly longer in the second case. The experiment may be varied by making use of all the vowel sounds taken irregularly as the stimulus, the subject responding by a signal to one only, as arranged beforehand. And of course other orders of stimulus may be used, either visual, the signal being made when a red light is shewn but not when other colours are shewn, or tactile, the signal being made when one part of the body is touched but not when other parts are touched, and the like.

In such experiments where the subject has to distinguish, to discriminate between two or more events, the prolongation of the reaction period is obviously due to the longer time required for the psychical processes taking place during what we have called the central stage. In the two cases, one without and the other with discrimination, not only are the afferent and efferent stages the same in both, but we have no reason to suppose that in the central stage is there any difference between the two cases as to the time taken up by the transformation of simple sensory impulses into perceptions, or as to that taken up by the will in gaining access to the motor apparatus and so starting the processes of the efferent stage; the delay takes place in the psychical processes intervening between these two parts, and the amount of delay is the measure of the time needed for the processes involved in the discrimination. This "discrimination period" has been found to differ in the same individual according to the sensation employed, visual, auditory, &c., and according to the kind of difference in the sensation which has to be discriminated, for instance in visual sensations between colours or between objects in different parts of the field of vision. In a series of observations made in this way, the discrimination period, i.e. the prolongation of the simple reaction period due to having to discriminate, was found to range from 0·011 sec. to 0·062 sec.

Another series of observations may be made in the following way. The signal being one made with the hand, the simple reaction period for a stimulus is determined with the signal given by the right hand. Two kinds of stimuli are then employed, both of the same order, two vowel sounds for instance, and the subject is directed to respond to one vowel with the right hand and to the other with the left hand. It is found, the subject being right-handed, that the reaction period is greater when the signal is made with the left hand. In this case the delay takes place not in the recognition of the effects of the stimulus, nor in the processes through which the will is formed upon that recognition; these are the same in the two cases; it takes place in the processes by which the will is brought to bear on the nervous motor apparatus for making the signal, on the cortical origin, for example of the pyramidal tract; these processes take a longer time in the case of the unaccustomed left hand than in the case of the usual right hand. In this way we obtain a measure of so to speak the volitional side of psychical processes.

In a somewhat similar way we may obtain a measure of the time required for perception. A strong sensation following too closely upon a weak one will prevent the psychical recognition of the weaker one. If, for instance, two or three letters in white on a black background be presented to the eye, and a large white surface be presented afterwards at an interval which is made successively shorter and shorter, it is found that when the interval is made very brief indeed the letters cannot be perceived at all. In proportion as the interval is prolonged, the recognition of the letters increases, until at an interval of about ·05 sec. they are fully and clearly recognized. That is to say, the time required for perception is in such a case of about that length.

The duration of all these psychical processes, as of the simple reaction period itself, varies of course under different circumstances, and the discrimination period may be conveniently used for measurements of the varying effects of circumstances. Practice shortens the discrimination period as it does the simple reaction period. One of the most powerful influences is that of attention. And it is stated that the shortening of the period is greater when the attention is concentrated on the making of the signal than when it is more especially directed to recognition of the stimulus; in other words, the volitional processes are more amenable than are the perceptive processes to the psychical action which we call attention. On the other hand, the period is distinctly prolonged if the observer be distracted by concomitant sensations. For example, the period for discriminating between two visual sensations is prolonged if powerful auditory sensations be excited at the same time.

The same method of measurement may be used in other ways and under other circumstances with reference to psychical processes. It must be remembered, however, that all such observations are open to many fallacies and need particular caution. It not unfrequently happens that false results are obtained; for instance, the subject, expecting the stimulus to be brought to bear upon him and straining his attention, makes the signal before the stimulus actually comes off. And the interpretation of the results obtained are in many cases very difficult; but it would be out of place to dwell upon these matters any further here.

SEC. 12. THE LYMPHATIC ARRANGEMENTS OF THE BRAIN AND SPINAL CORD.

§ 693. *The Membranes of the Brain and Spinal Cord.* The cerebro-spinal canal is lined by a tough lamellated membrane, composed of connective tissue with a small amount of elastic networks, called the *dura mater*, which, somewhat closely adherent to the walls of the cranial cavity, is separated from those of the vertebral canal by a considerable space, containing blood vessels, especially large venous sinuses, and some fat. It may be considered as a development of the periosteum lining the cerebro-spinal cavity. It sends tubular sheaths for some distance along the several cranial and spinal nerves; and forms between the cerebral hemispheres, in the longitudinal fissure, a conspicuous sickle-shaped vertical fold, the *falx cerebri*, as well as a smaller horizontal or oblique fold between the cerebellum and cerebrum known as the *tentorium*.

The vascular *pia mater* is closely attached to the surface of the brain and spinal cord, dipping down as we have seen into the ventral or anterior fissure of the cord as well as into the fissures of the brain. Sheath-like investments of pia mater are continued along the several nerves as they leave the cerebro-spinal cavity; and in the vertebral canal an imperfect partition half-way between the dorsal and ventral surfaces of the cord is furnished by a membrane of connective tissue which, continuous along its whole length with the pia mater, is attached to and fused with the dura mater at intervals only, namely, between the successive nerve roots. Since its outer edge has thus a toothed appearance, this membrane is called the *ligamentum denticulatum*. Between the pia mater next to the brain and cord and the dura mater next to the bony walls is a cavity, which is divided into two by a thin membrane, *the arachnoid*, composed of interwoven bundles of connective tissue. The space between the arachnoid and the dura mater is called the *subdural space*, and the space between the arachnoid and the pia mater is called the *subarachnoid space*. When the brain is exposed by removing the roof of the skull and slitting open the dura mater, the subdural space is laid bare, and the arachnoid is seen stretching over the pia mater; in the vertebral canal the arachnoid lies close to the dura mater, so that usually, when the dura mater is slit open and turned back, the arachnoid is carried with it and the cavity exposed is that of the subarachnoid space. The arachnoid, like the dura mater and the pia mater, is continued for some distance over the nerves as they leave the cerebro-spinal cavity; so that each nerve at its exit is surrounded by a tubular prolongation of the subdural space, and within this a similar tubular prolongation of the subarachnoid space.

The subdural space is broken up to a slight extent only by bridles carrying nerves and blood vessels, especially venous sinuses, between the pia mater and dura mater, and, over the surface of the brain, by villus-like projections of the arachnoid, called Pacchionian glands, some of which pierce the venous sinuses of the dura mater. It is lined throughout, both on its dural and on its arachnoid wall, by an epithelium of flat epithelioid cells, and may be compared to a serous cavity such as that of the peritoneum. Like the serous cavities it contains normally a small quantity only of fluid, and its size is potential rather than actual.

The subarachnoid space on the other hand is, especially in certain regions, such as the dorsal portions of the vertebral canal and the base of the brain, much broken up by bridles of connective tissue passing from it to the pia mater, as well as by a network or sponge-like arrangement of bundles of connective tissue lying immediately beneath itself, and giving it when viewed from below a honeycomb or fenestrated appearance. The under surface of the membrane itself as well as all the trabeculae of the sponge-work and the bridles are covered with an epithelium of flat epithelioid cells, which is continued also over the pia mater and the ligamentum denticulatum, and lines the tubular sheath-like prolongations of the space along the issuing nerve roots. The subarachnoid space therefore, like the subdural space, may be regarded as a serous or large lymphatic space, but it is an actual not a mere potential space; it always contains an appreciable quantity of fluid, which however is not ordinary lymph, but is furnished in a particular way, and deserves special study. To understand the nature and origin of this *cerebro-spinal fluid,* as it is called, we must turn to some special arrangements of the pia mater.

§ **694.** The pia mater proper, consisting of interwoven bundles of connective tissue, with some elastic fibres and a considerable number of connective tissue corpuscles, serves as we have said as the bearer of blood vessels to the nervous structures which it invests. The small arteries as they pass into the nervous substance by the way of the septa are surrounded by perivascular lymphatic canals with which spaces in the neuroglial groundwork both of the brain and spinal cord, especially spaces surrounding the larger nerve cells, are continuous. As is the case with other tissues, so with the central nervous system, the several elements of the tissue are bathed with lymph derived from the blood; and this, oozing through the spaces into the perivascular canals and the other lymphatic vessels of the pia mater, makes its way into the subarachnoid space; but the fluid in the subarachnoid space has other sources besides.

The roof of the fourth ventricle is, as we have said (§ 601) reduced to a single layer of non-nervous columnar epithelium, which appears as a mere lining to the pia mater overlying it. In the hinder part of the ventricle this roof is perforated by a distinct narrow oval orifice, the *foramen of Majendie.* By this orifice, which passes right through both the pia mater and the underlying layer of epithelium, the cavity of the fourth ventricle, and so the whole series of cavities derived from the original medullary canal, the lateral and third ventricles, the aqueduct, and the central canal of the spinal cord, are made continuous with the subarachnoid space. There are also other less conspicuous communications between the subarachnoid space and the fourth ventricle. Hence the cerebro-spinal fluid is made common to all these cavities, and is furnished not only by the pia mater investing the outside of the brain and spinal cord, but also, and indeed probably to a larger extent, by the epithelium lining the several cavities of the cerebro-spinal axis, especially perhaps by those portions of that epithelium which coat the processes of pia mater projecting into those cavities at certain places.

We saw previously (§ 602) that a large fold of the pia mater, carrying in with it the thin non-nervous epithelium which alone represents at the place the original wall of the medullary canal, is thrust inward at the transverse fissure of the brain, beneath the fornix, to form the velum interpositum, thus supplying a roof to the third ventricle, and that it thence projects into each lateral ventricle as the choroid plexus of each side, reaching from the foramen of Monro in front along the edge of the fornix to the tip of the descending horn. The velum being a fold of the pia mater consists theoretically of two layers, and between the upper dorsal layer and the lower ventral layer, lies a thin bed of connective tissue carrying arteries forwards from the hind edge of the corpus callosum, and similarly carrying veins backwards; these vessels supply the choroid plexus with an abundant supply of blood. In the choroid plexus, the folded pia mater is developed into a number of villus-like processes, the primary processes bearing secondary ones. Each process consists, like a villus, of a basis of connective tissue, in which the blood vessels end in close set capillary loops, covered with an epithelium. The epithelium, though continuous with the rest of the epithelium lining the lateral ventricle, and thus as we have said shutting off the lateral from the third ventricle (except at the foramen of Monro), and though like it derived from the wall of the original medullary canal, is different in structure. Over the ventricle generally the epithelium consists of ordinary short columnar, apparently ciliated, cells, with more or less transparent cell-substance; the cells over the choroid plexus are cubical, often irregular in form, and their cell-substance is loaded with granules, some of which are pigmentary. They have very much the appearance of 'active' secreting cells; and indeed a branched process of the plexus may be compared to an everted alveolus of a secreting gland, with the epithelium outside and the blood vessels within. It cannot be doubted that these cells play an important part in secreting into the cavity of the ventricle fluid which, passing thence by the foramen of Monro into the third and so into the fourth ventricle, finds its way by the foramen of Majendie into the subarachnoid space.

As the velum overhangs the third ventricle it sends down vertically two longitudinal linear fringes, which, resembling in structure the choroid plexuses of the lateral ventricle, are called the choroid plexuses of the third ventricle. From the roof of the fourth ventricle there hangs down on each side a similar linear fringe, the choroid plexus of the fourth ventricle, which is especially developed at its front end beneath the overhanging cerebellum. These subsidiary choroid processes doubtless assist in furnishing cerebro-spinal fluid, but their share is small compared with that of the main choroid plexuses of the lateral ventricle.

§ 695. *The Cerebro-spinal Fluid.* The specimens of cerebro-spinal fluid which have been examined as to their composition are not quite comparable with each other, since while some (such as those obtained from cases where a fracture of the base of the skull has placed the subarachnoid space at the base of the brain, where it is largely developed, in communication with the external meatus, and the fluid escapes by the ear) may be regarded as normal, others (such as those obtained from cases of hydrocephalus where the ventricles contain an unusual quantity of fluid, or from cases of spinal malformations) must be considered as abnormal. In most of the more complete analyses, the fluid examined has belonged to the latter class; and the following statements apply, strictly speaking, to them alone.

With this caution we may say that cerebro-spinal fluid is a transparent, colourless or very slightly yellowish fluid, of faint alkaline reaction, free from histological elements. The specific gravity is about 1010 or less, the amount of solids being on an average 1 p.c. Of these by far the greater part, ·8 or ·9 p.c., is supplied by salts, the total quantity of which as well as the relative amount of the several constituents being about the same as obtain in blood and lymph. The comparative deficiency of solids is due to the scantiness of the proteids, which rarely exceed ·1 p.c. These are chiefly globulin and a form of albumose, or even peptone; albumin is said to be generally absent. The fluid, save apparently in exceptional cases, does not clot, and contains neither fibrogenous factors, nor fibrin ferment. It very frequently contains a substance which like dextrose reduces Fehling's solution but which is not a sugar; it appears to be pyrocatechin or a closely allied body.

Seeing that a fluid of such a composition is of a different nature from ordinary lymph, furnished entirely in the ordinary way, we might be inclined to infer that probably a very large part of the whole mass of the fluid is furnished by the secreting epithelium of the choroid plexus. But it must be borne in mind, that the foregoing analyses refer chiefly to fluid appearing under abnormal circumstances, and it would be hazardous to draw any wide inference from them. We have little or no exact experimental evidence as to how much fluid is actually secreted by the choroid plexuses; and if the fluids which have been analyzed do represent a mixture of ordinary lymph supplied through the pia mater with the peculiar secretion of the choroid plexus and cerebro-spinal canal, some further change beyond the mere mingling of the two fluids is needed to explain the remarkable absence of albumin which has been so strongly insisted upon by various authors.

§ **696**. We may fairly suppose that during life the fluid is continually being supplied, from the one source or the other; but we have no very exact knowledge as to the rate at which it is furnished. In the dog, the fluid has been observed to escape at a rate varying very largely under different circumstances, and ranging from 1 c.c. in 40 minutes to as much as 1 c.c., in 6 minutes, the total quantity discharged in 24 hours varying from 36 c.c. to 240 c.c. In the cases of fracture of the base of the skull mentioned above, a very considerable flow has been frequently observed; but it may be doubted whether the abnormal circumstances of such cases have not raised the secretion above the normal. The rate of flow was found in the dog to be much increased by the injection of substances (normal saline solution) into the blood, but to be relatively little influenced by artificial heightening of arterial pressure. This has been put forward as indicating that the fluid is chiefly furnished as a secretion and not as an ordinary transudation of lymph; but it cannot be regarded as affording a valid argument. The pressure under which the fluid exists is also very variable; it is closely dependent on the vascular arrangements of which we shall have to speak presently. In the dog the average pressure has been estimated at about 10 mm. of mercury.

If the fluid is thus continually formed it must always find a means of escape. This is probably supplied by the tubular prolongations of the subarachnoid space along the nerve roots; these are continuous with the lymphatic vessels of the nerves, and so with the lymphatics of the body generally; and in the skull, the passages of this kind along the cranial nerves, especially along the two optic nerves into the orbits, afford a ready means of escape. It is also urged that some of the fluid escapes through the Pacchionian glands directly into the blood of the venous sinuses. In a dead body fluid introduced into the subarachnoid space through an opening over the bulb, disappears at even a very low pressure with great rapidity. The circumstances then are, however, not the same as in life; and the few experiments which have been made seem to shew that, during life, a somewhat high pressure is required to secure the escape of fluid introduced in addition to that naturally secreted. Thus it is stated that when in a dog normal saline solution is introduced into the subarachnoid cavity at the lower end of the spinal cord very little resorption takes place so long as the pressure remains as low as about 10 c.c. of mercury; as the pressure is increased beyond this resorption quickly increases. But it may be doubted whether the resorption of added fluid is a fair test of the escape of fluid naturally present; and the experiment is of value rather as shewing simply that there are means of escape than as affording a measure of the rate of escape. Besides, the immediate effects of applying pressure at the caudal end of the spinal cord are not the same as those of applying pressure within the skull.

The rate of possible escape is not without importance as regards the mechanical importance of the cerebro-spinal fluid. Thus it has been urged that when an extra quantity of blood is driven into the skull, any injurious intercranial compression is prevented, not only by the transference of a corresponding quantity of cerebro-spinal fluid through the foramen of Majendie from the cranium into the spinal canal, the walls of which are less rigidly complete, but also by the direct escape of the fluid from the cavity of the skull along the cranial nerves in the manner described. It has also been urged that the fluid at the base of the skull, in the large subarachnoid spaces of which it gathers in larger quantity than elsewhere, acts as a sort of protective water cushion to the delicate cerebral substance, and that, in general, the presence of the fluid is mechanically useful to the welfare of the brain, removal of the fluid by aspiration being said to lead to hæmorrhage from the pia mater and to various nervous disorders. But our knowledge as to the part which the fluid plays is at present very imperfect; and its very peculiar chemical characters suggest that it has some chemical as well at least as mechanical functions.

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SEC. 13. THE VASCULAR ARRANGEMENTS OF THE BRAIN AND SPINAL CORD.

§ 697. The blood vessels reach the nervous structures by means of the pia mater. In the spinal cord arteries coming from the vertebral, intercostal and other arteries, and travelling along the nerve roots join the pia mater, and then through the fissures and septa reach all parts of the cord; but as we have previously remarked the capillary network is much denser, and therefore the blood supply much greater in the grey than in the white matter. The veins, also gathered up along the septa and fissures into the pia mater, those coming from the grey matter forming, before they reach the external pia mater, a conspicuous longitudinal vein on each side of the posterior grey commissure, pass from the pia mater to the large venous sinuses of the dura mater and so to adjoining veins.

In the brain two important features of the distribution of the arteries deserve special attention. In the first place, the quadruple supply by the right and left vertebral and internal carotid arteries is made one by remarkable anastomoses forming the *circle of Willis.* The right and left vertebral arteries entering the vertebral canal at the level of the 6th cervical vertebra, and running forwards towards the brain, join beneath the ventral surface of the bulb to form the single median basilar artery. This, after giving off branches to the bulb, cerebellum, and pons divides into the right and left posterior cerebral arteries. Each internal carotid entering the skull reaches the base of the brain in the region of the floor of the third ventricle, and, passing ventral to and athwart the optic tract, gives off the large and important middle cerebral artery along the fissure of Sylvius, and then, turning forwards and towards the median line, passes dorsal to the optic nerve to end in the anterior cerebral artery. Just however as it gives off the middle artery, it sends backwards, inclining to the middle line, a relatively large branch, the posterior communicating artery, which joins the posterior cerebral near the origin of this from the basilar artery. Moreover, the two anterior cerebral arteries soon after they have crossed the optic nerves, just as they are about to run straight forwards along the frontal lobes, are joined together by a short wide branch, the anterior communicating artery. In this way the vertebral arteries through the basilar artery join with the carotid arteries to form around the optic chiasma beneath the floor of the third ventricle an arterial circle, the circle of Willis.

Blood can pass along this circle in various ways; from the basilar artery along the right posterior communicating artery to the right internal carotid, and so by the right anterior cerebral artery and anterior communicating artery to the left side of the circle, and similarly from the basilar artery along the left side to the right, or from the right or from the left carotid through the circle, to the right hand or to the left hand in each case. Since the channel of the circle is a fairly wide one, the passage in various directions is an easy one; all the vessels radiating from the circle, including the basilar artery and its branches, can be supplied by the carotids alone, or by the vertebrals alone, or even by one carotid or one vertebral alone. In this way an ample supply of blood to the brain is secured in the face of any hindrance to the flow of blood along any one of the four channels.

In what may perhaps be considered the usual arrangement, the calibre of the posterior communicating arteries is rather smaller than the other parts of the circle, so that, other things being equal, most of the vertebral blood will pass by the posterior cerebral arteries, while the carotid blood passes to the middle and anterior cerebral arteries; but many variations are met with. We may also here perhaps call to mind the fact that the left carotid coming off from the top of the aorta, offers a more straight path for the blood than does the right carotid which comes off from the innominate artery.

Another special feature of the arterial supply to the brain is that the three large cerebral arteries, posterior, middle and anterior, are distributed almost exclusively to the cortex and to the subjacent white matter, while the deeper parts of the hemisphere, the nucleus caudatus, thalamus and the like, with the capsule and other adjoining white matter are supplied by smaller arteries coming direct from the circle of Willis, or from the very beginnings of the three cerebral arteries. It is stated that these two systems make no anastomoses with each other; but this appears to vary much in different individuals. We may add that the anterior cerebral artery supplies the cortex of the dorsal aspect of the frontal lobe as well as the front and middle portions of the whole mesial surface of the hemisphere; while the middle cerebral, always large, is distributed to the side of the brain, that is, the parietal lobe, with the ventral part of the frontal lobe and the dorsal part of the temporal lobe; the posterior cerebral supplying the rest of the cortex, that is to say, the occipital lobe including the hind part of the mesial surface of hemisphere, together with the ventral part of the temporal lobe. The distribution of these arteries therefore does not correspond to functional divisions, for while the middle cerebral supplies a large part of the motor region, it does not supply the whole of it, and does supply parts outside it. Though the small arteries as they run in the pia mater on the surface of the cortex anastomose freely, there is very little anastomosis between the small arteries which leaving the pia mater dip down into the substance of the brain; hence when these latter arteries are blocked, the nutrition of the part of the cortex supplied by them is apt to be impaired.

§ **698**. The venous arrangements of the brain have very special characters.

Along the upper convex border of the sickle-shaped fold of dura mater, the falx cerebri, is developed a large venous sinus, the *superior longitudinal sinus.* This, triangular in section, increasing in calibre from before backwards, is a sinus, not a vein; its walls are formed of nothing but connective tissue lined with epithelium, muscular elements being entirely absent. Though its channel is broken by bridles of connective tissue passing across it, it possesses no valves, and indeed these are absent from all the sinuses and veins of the brain. Most of the blood returning from the cortex and subjacent white matter is carried into this sinus by veins, the mouths of which are for the most part directed forwards, that is to say, against the direction of the blood stream. Along the lower concave border of the falx is a similar sinus, the *inferior longitudinal sinus,* which however is small and into which relatively few veins open.

From the deeper parts of the brain, and especially from the choroid plexus, blood is conveyed by the *veins of Galen* along the velum interpositum to the transverse fissure, where the veins of Galen join the inferior longitudinal sinus to form the *straight sinus.* This, running along the line formed by the intersection of the vertical falx with the (more or less) horizontal tentorium, joins the end of the superior longitudinal sinus to form the reservoir or cellar, called the *torcular Herophili,* from which the *lateral sinus*, passing on each side along the convex border of the tentorium and gathering veins from the cerebellum and hind regions, as well as from the base of the brain, delivers the blood into the internal jugular vein.

It should be added that veins from the nose and, through the ophthalmic veins, from the face join the veins and sinuses of the brain, and that the so-called emissory veins pass through the cranium from the scalp to the superior longitudinal and lateral sinuses.

The channels for the venous blood of the brain are therefore not veins but sinuses, not so much tubes for maintaining a uniform current as longitudinal reservoirs, which while affording an easy onward path can also be easily filled and easily emptied, and in which the blood can move to and fro without the restrictions of valves. This arrangement is correlated to the peculiar surroundings of the brain, which is not like other organs protected merely by skin or other extensible and elastic tissue, but is encased by a fairly complete inextensible envelope, the skull. As a consequence of this, when at any time an extra quantity of blood is sent from the heart to the brain, room must be made for it by the increased exit of the fluids already present. For any pressure on the brain-substance beyond a certain limit is injurious to its welfare and activity, as is seen in certain maladies, where blood passing by rupture of the blood vessels out of its normal channels remains effused on the surface of the brain or elsewhere, and thus taking up the room of the proper brain-substance leads, by 'compression' as it is called, to paralysis, loss of consciousness, or death. Some room may, as we have seen (§ 696), be provided by the escape of cerebro-spinal fluid from the skull. But, within the limits of the normal cerebral circulation, the characteristic venous sinuses especially serve to regulate the internal pressure; they form temporary reservoirs from which a comparatively large quantity of blood can be rapidly discharged from the cranium, the flow from the sinuses being greatly assisted by the low or negative pressure obtaining in the veins of the neck at each inspiratory movement of the chest.

§ **699**. The supply of blood to the brain seems at first sight not to correspond to the importance of this the chief organ of the body. In the rabbit it would appear that hardly more than one per cent. of the total quantity of the blood of the body is present at any one time in the brain, a quantity but little more than half that which is found in the kidneys; and while the weight of blood in the brain at any one time amounts to about five per cent. of the total weight of the organ, being about the same as in the muscles, in the kidney it amounts to nearly twelve per cent., and in the liver to as much as nearly thirty per cent. Making every allowance for the relative small size and functional importance of the rabbit's brain, the blood-supply of even the human brain must still be small; and making every allowance for rapidity of current, the interchange between the blood and the nervous elements must also be small. In other words, the metabolism of the brain-substance is of importance not so much on account of its quantity as of its special qualities.

The circulation in the brain may be studied by help of various methods. A manometer may be connected with the *peripheral* end of the divided internal carotid artery, a second manometer being attached in the usual way to the central portion. Since the peripheral manometer records the blood-pressure in the circle of Willis transmitted along the peripheral portion of the carotid artery, variations of pressure in the circle of Willis may thus be studied; and a comparison of the peripheral with the central manometer will indicate what general changes are taking place in the circulation through the brain. Thus a fall of pressure in the peripheral manometer unaccompanied by any corresponding fall in the central manometer would shew that the "peripheral resistance" in the brain was being lowered, in other words, that the vessels were being dilated.

In another method, in the dog, the outflow of venous blood from the lateral sinus through the posterior facial vein has been measured. The freedom with which blood passes along the sinuses justifies the assumption that the outflow through the open vein gives an approximate measure of the rate of flow under natural conditions; still the results are only approximate, and besides, the continued loss of blood introduces error.

A third method is a plethysmographic one. The skull is made to serve as the box of the plethysmograph or oncometer (§ 410); a small piece of the roof having been removed by the trephine, a membrane is fitted to the hole, and the movements of the membrane are recorded by help of a piston and lever or directly by a lever. In young subjects, the fontanelle, or portion of the cranium not yet ossified, may be utilized as a natural membrane, and its movements recorded in a similar manner. When the instrument is fitted to the hole in a water-tight manner, this method records variations in internal pressure; and we may take it for granted, unless otherwise indicated, that greater or less pressure is due to more or less blood passing to the brain. But the amount of pressure brought to bear on the recording instrument will also depend on the readiness with which the cerebro-spinal fluid escapes from the cavity of the skull; if there be a hindrance to the escape, or on the other hand an increased facility of escape, the same increase of supply of blood will produce in one case a less, in the other a greater movement of the lever. If the membrane be attached loosely to the hole so as to allow free escape of the cerebro-spinal fluid, the lever practically resting on the surface of the cerebral hemisphere, the method records variations in the dorso-ventral diameter of the hemisphere, and these may be taken as measuring variations in the volume of the brain and so in the blood supply. In neither form, however, does the method by itself give us all the information which we want. An increase of blood in the brain, and therefore an expansion of the brain, and so a movement of the recording instrument, may result either from a fuller arterial supply or from hindrance to the venous outflow; the former condition is, at least in most cases, favourable to, the latter always and distinctly injurious to, the activity of the nervous structures; hence the teachings of the lever must be corrected by a simultaneous observation of the general arterial pressure and of the blood-pressure in the veins of the neck. Moreover, the argument which we used (§ 417) in reference to the kidney may be applied here and probably with equal force, namely, that the value of the blood stream for the nutrition of the tissue is dependent not alone on the amount of blood-pressure, but also and especially on the rapidity of the flow; indeed this second factor is of particular importance in view of the need of supplying the nervous elements with an adequate interchange of gases. Now of the rapidity of flow the plethysmographic method can give us indirect information only.

§ **700.** By one or other or all of these methods, certain important facts have been made out. The volume of the brain, as determined by the amount of blood present in it, is continually undergoing changes brought about by various causes. Each heart-beat makes itself visible on the cerebral as on the renal plethysmographic tracing, and as we have seen in speaking of respiration, the diminution of pressure in the great veins of the neck during inspiration leads to a shrinking, and the reverse change during expiration to a swelling of the brain. The plethysmograph also shews variations, larger and slower than the respiratory undulations, and brought about by various causes, such as the position of the head in relation to the trunk, movements of the limbs, modifications of the respiratory movements, and apparently phases of activity of the brain itself, as in waking and sleeping; undulations corresponding to the Traube-Hering variations (§ 387) of blood-pressure may not unfrequently be observed.

All the various methods shew that the flow through the brain is largely determined by a vaso-motor action of some kind or another. And this we might indeed infer from ordinary experience. When the head is suddenly shifted from the erect to a hanging position, there must be a tendency for the blood to accumulate in the cranial cavity, and conversely when the head is suddenly shifted from a hanging to an erect position, there must be a tendency for the supply of blood within the cranium to be for a while less than normal. Either change of position, and especially perhaps the latter, would lead to cerebral disturbances, which in turn would in ourselves be revealed by affections of our consciousness. That a perfectly healthy, and especially young organism whose vaso-motor mechanisms are at once effective and delicately responsive, can pass swiftly from one position of the head to the other without inconvenience, whereas those in whom the vaso-motor mechanisms have by age or otherwise become imperfect are giddy when they attempt such rapid changes, is in itself adequate evidence of the importance of the vaso-motor arrangements affecting the circulation through the brain. The several methods agree in shewing that increased general arterial pressure, such as that for instance induced by stimulation of a sensory nerve, leads to a greater flow of blood to the brain; the volume of the brain is increased and the venous outflow by the lateral sinus is quickened. Conversely, a lowering of arterial pressure leads to a lessened flow of blood to the brain.

Seeing that the cerebral arteries have well-developed muscular coats, the basilar artery in fact being conspicuous in this respect, one would be led to suppose that the brain possessed special vaso-motor nerves of its own; and recognizing the importance of blood supply to rapid functional activity one would perhaps anticipate that by special vaso-motor action, the supply of blood to this or that particular part of the brain might be regulated apart from changes in the general supply. The various observations, however, which have hitherto been made have failed to demonstrate with certainty any such special vaso-motor nerves or fibres directly governing cerebral vessels. It would be hazardous to insist too much on this negative result, especially since the observations have been chiefly directed to the nerves of the neck, the experimental difficulties of investigating the presence of vaso-motor fibres in the cranial nerves being very great. Still it may be urged and indeed has been urged that the flow of blood through the brain is so delicately responsive to the working of the general vaso-motor mechanism just because it has no vaso-motor nerves of its own. In such an organ as the kidney, an increase of general blood-pressure, as we have more than once insisted, may or may not lead to a greater flow through the kidney according as the vessels of the kidney itself, through the action of the renal vaso-motor nerves, are dilated or constricted; and, as we have seen, a constriction of the renal vessels may be one of the contributors to the increased general pressure. In the brain, on the other hand, an increase of general arterial pressure seems always to lead to increase of flow. Thus in the Traube-Hering undulations just mentioned, the expansions of the brain are coincident with the rises of the general pressure, whereas in the normal kidney and in other organs the local Traube-Hering undulation reverses the general one, the shrinkings are synchronous with the rises of pressure, the local constriction being one of the factors of the general rise. It is argued, that in the absence of vaso-motor nerves of their own, the cerebral vessels are wholly, so to speak, in the hands of the general vaso-motor system, so that when the blood-pressure is high owing to a large vaso-constriction in the abdominal viscera, more blood must necessarily pass to the brain, and when again the blood-pressure falls through the opening of the splanchnic flood-gates (§ 173) less blood necessarily flows along the cerebral vessels. And indeed one may recognize here a sort of self-regulating action; for diminishing the supply of blood to the vaso-motor centre in the bulb acts, as we know, as a powerful stimulus in producing vaso-constriction, and so leads to a rise of blood-pressure; but this very rise of blood-pressure drives more blood to the brain, including the bulb, and thus the injurious effects to the brain threatened by an anaemic condition are warded off by the very beginning of the anaemia itself. All these advantages are, however, quite compatible with the coexistence of special vaso-motor mechanisms.

§ **701.** Moreover the flow of blood to, and consequent change in the bulk of, the brain, and indeed the flow of blood through the brain, as measured by the venous outflow, may be modified independently of changes in the general blood-pressure. For instance, stimulation of the motor region of the cortex quickens the venous outflow, without producing any marked change in the general blood-pressure; this feature becomes very striking at the onset of epileptiform convulsions when these make their appearance. It is difficult not to connect such a result of functional activity with some special vaso-motor nervous arrangement comparable to that so obvious in the case of a secreting gland. Again, it has been observed that certain drugs have an effect on the volume of the brain, quite incommensurate with their effect on the vaso-motor system; thus in particular the injection into the general blood stream of a weak acid produces a large and immediate expansion of the brain, while the introduction of a weak alkali similarly gives rise to similar considerable shrinking. It is suggested that these effects are produced by the acid or alkali acting directly on the muscular coats of the minute arteries and so leading to relaxation or contraction respectively. In treating of the chemistry of nervous substance (§ 72) we stated that "the grey matter of the central nervous system is said to be slightly acid during life and to become more acid after death." Recent observations go to shew that the grey matter of the cortex is faintly alkaline during life and under normal conditions, but becomes acid after death or when its blood-supply is interfered with; and it has been urged that nervous grey matter like muscular substance developes acidity during activity, as well as upon death, the acidity being probably due in each case to some form of lactic acid. And just as it has been suggested that the dilation of the minute arteries of a skeletal muscle, accompanying or following the contraction of the muscle, is brought about by the acid generated during the contraction causing a relaxation of the muscular coats of the minute arteries, so it has been suggested that a similar acidity, the product of nervous activity, similarly leads in nervous tissue to a dilation of the vessels of the part. The existence of special vaso-motor mechanisms would, however, afford a more satisfactory explanation of these and other phenomena; in spite of the negative results so far obtained, the matter is obviously one needing further investigation. Meanwhile we have abundant evidence that, however brought about, the flow of blood through the brain, and probably through particular parts of the brain, is varied in accordance with the needs of the brain itself and the events taking place elsewhere in the body.

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